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PHYTOPATHOLOGY

VOLUME XII NUMBER 12

DECEMBER, 1922

II. SEPTORIA DISEASES OF WHEAT[1]

GEORGE F. WEBER

WITH PLATES XXIII TO XXXVI AND SIXTEEN FIGURES IN THE TEXT

On wheat there are two diseases caused by different species of Septoria, namely, *S. nodorum* Berk. and *S. tritici* Desm. The one, caused by *S. nodorum*, attacks the glumes most commonly producing brown blotches on them, hence it has been called "Glume Blotch." This usage will be followed in this paper. This disease may also attack the rachis, culms and leaves. The other disease, caused by *S. tritici*, attacks the leaves only, producing conspicuous light colored lesions in which the dark colored pycnidia are prominent and produce a speckled appearance. On account of this outstanding characteristic the name "Speckled Leaf Blotch" is here suggested for this disease. This name will be used in this paper.

GLUME BLOTCH OF WHEAT

INTRODUCTION

A Septoria disease found upon the leaves and glumes of wheat has been reported recently as a serious disease of wheat (26). The fungus was reported present over large areas in different sections of the country, and in certain wheat growing districts serious losses in grain yield have been recorded. It is caused by the parasitic fungus *Septoria nodorum* Berk. The organism attacks different parts of the plant causing irregular shaped areas to become discolored and dead. Heads of wheat are especially seriously attacked and become blackened, beginning at the tips of the outer glumes and working toward the base.

THE DISEASE

Hosts

This organism was first found on wheat by Berkeley (2) in 1845, and by Passerini (25) in 1879. Since then it has been reported wide spread

[1] This is the second of three articles by the author on the Septoria diseases of cereals and some of the grasses. The first appeared in Phytopathology, number 10, volume 12.

conforming to the cultivation of the wheat plant. Sorauer (31) reported it on speltz and wheat. Neuen-Lemarie (22) listed wheat, barley, rye and oats as host plants of this organism. The writer has conducted a series of inoculation experiments in an effort to gain some knowledge as to its host range and as a result has found that only wheat species, rye and *Poa pratensis* become infected while species of barley and oats and a number of related grasses remain free from the disease. It is peculiar, however, that in the case of rye only the leaves become infected, while in the cases of wheat and *Poa pratensis* all parts above ground are susceptible. These experiments will be taken up in detail later in this paper.

Geographical Distribution

Septoria nodorum Berk. was first reported in England by Berkeley (2). Later it was reported in northern Italy by Passerini (25). It was also reported in other parts of Italy by Cavara and Comes according to Voglino (36). Eriksson (12) observed this disease in Sweden. It was reported in Switzerland by Baltshauser according to Voglino (36) and from different parts of Germany by Frank (14). Selby (30) and Townsend (33) describe its appearance in Ohio and Maryland respectively. Rosen (28) reported the fungus locally in parts of Arkansas. Güssow (16) reported the disease as being general and common in Europe. Marchal and Foëx (20) found it in France near Toulouse. Sutton (32) published a short note on the occurrence of the disease in western Australia.

In the United States the disease is rather generally distributed. It has been reported as common in all wheat growing regions, which includes the Mississippi basin and smaller areas on the Atlantic and Pacific coasts. It has been reported most prevalent in the South and and East Central States of the United States.

Economic Importance

No serious damage to the wheat crop was reported as being caused by this fungus until Townsend (33) reported serious losses in Maryland. He stated that the yield of certain fields was reduced from 30 or 35 bushels per acre to 15 bushels per acre and that the kernels were very much shrivelled. Voglino (36) observed that the wheat fields in Piedmont were often attacked by this fungus and that severely infected heads always produced shrivelled kernels of abnormal structure. Observations and notes of the disease in England by Berkeley (2) and Massee (21) state that it was abundant in the wheat fields and caused

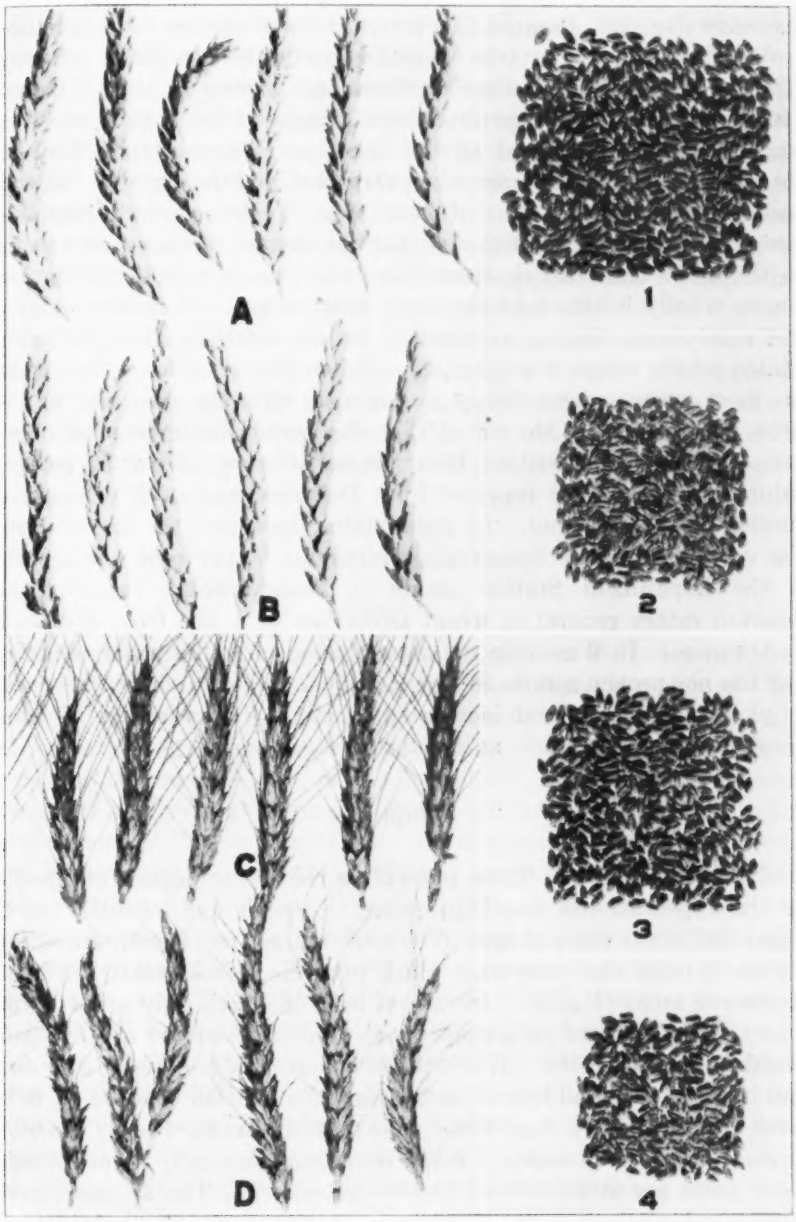

Fig. 1. Red Wave (A and B) and Turkey (C and D) wheat grown in greenhouse A and C healthy; 1 and 3 grain from similar heads of same varieties respectively. B and D following inoculation with *S. nodorum;* 2 and 4 grain from heads similarly inoculated.

extensive damage. Sorauer (31) stated that the quality of the seed was badly affected by the attacks of this fungus on the host plant. Schmitz (29) reported serious damage to wheat in all parts of Italy. Güssow (16) considered no loss resulted from attacks of the fungus on wheat since it rarely penetrated to the kernels. Delacroix and Maublanc (9) report very little damage where they observed the disease. Marchal and Foëx (20) found the disease near Toulouse but reported no damage. Sutton (32) concluded that the disease was most destructive on the nodes and least destructive on the glumes, that the injury was almost wholly confined to the early sown crops, and that the disease was most serious during wet years. He did not think that the milling quality of the wheat was impaired. Rosen (28) considered this disease the most serious wheat disease in Arkansas with the exception of *Puccinia triticina* Erik. He stated that the kernels were reduced in size and shrivelled. In 1919 in Plant Disease Survey (26) a .25 per cent reduction in yield was reported from Delaware and a .5 per cent reduction from Maryland. In most states, however, the loss reported was very slight. Infection ranging from 50 to 90 per cent was reported in the Experiment Station plants in Pennsylvania. Infection was reported rather general in wheat fields east of a line from Minnesota to Arkansas. In Wisconsin the disease has been found widely scattered but has nor proven serious in any locality. Figure I shows the results in yield, of controls and inoculated heads of two varieties of wheat grown in the greenhouse at Madison, Wisconsin.

Symptoms

Glumes and lemmas. These parts show the first indication of infection by the appearance of small, irregular, brownish spots, usually on the upper half of the outer glume. The spots enlarge and become chocolate-brown in color and very soon black pycnidia appear scattered in the discolored areas (Fig. 2). In case of light infection only a few glumes may become diseased on a single head. In such case the others remain healthy until maturity. When the heads are badly diseased the outer and inner glumes and lemma become infected and all exposed parts become dark brown in a short time. The pycnidia are then easily observed.

Rachis, culm and nodes. When conditions especially favor infection these parts are attacked and become discolored. The attacked nodes of the rachis become almost black and the nodes of the culm become dark brown. Both of these parts become dotted with pycnidia. The culm is colored light brown and the spots are large, often covering the

greater part of certain internodes. Pycnidia have not been observed upon the discolored areas of the culm.

Leaves. Infection of the leaf resulted in the appearance of yellowish spots 8 or 9 days after inoculation. These spots become light colored and then the tissues become dry. As the drying took place pycnidia appeared very sparsely and scattered. As the central part of the spot dried out it became lighter colored. Often these spots were almost white in the center surrounded by a brownish area which marked the limit of the living tissue. Often numerous spots coalesced and when infection was heavy and growing conditions favored the development of the fungus they involved most of the leaf, killing it very soon. The leaf turned brown, the edges often curling backward. The pycnidia were rather uniformly distributed over both surfaces of the leaf and upon close examination were found to be seriately arranged. The pycnidia on the leaves were in every way similar to those found on the glumes, rachis, and nodes.

CAUSAL ORGANISM

Taxomony

This disease was first described by Berkeley (2) on the nodes and internodes of wheat and the causal organism named *Septoria nodorum*. Passerini (24) described a disease on the glumes of wheat in Parma, Italy, and named the organism *Septoria glumarum*. The latter binomial has been generally accepted and is in common use in literature at present. Kühn (18) described an organism on the glumes of wheat in Germany which he named *Phoma hennebergii*. Upon examination of this material later Berlese and Voglino (3) found the organism to be *Macrophoma* (*Cylindrophoma*) *hennebergii*. Voglino (36) stated that Frank and Kirchner reported the disease as common in Germany, and also that Kirchner and Boltshauser considered it very similar to *Septoria glumarum* Pass. Because of the resemblance between Kühn's description and the description of Passerini, Voglino, although unable to examine the specimen of Kühn, thought that *Machrophoma* (*Cylindrophoma*) *hennebergii*. Kühn should be included with *Septoria glumarum* Pass. Grove (15) examined this disease on wheat from Australia and England and later compared these specimens with Berkeley's original collection in Kew herbarium. He concluded that the diseases on culm, node and glumes were caused by the same species of fungus and that the diseased material from England and Australia was the same as that which Berkeley deposited in Kew. Rosen (28) stated that the disease found on wheat in

Arkansas conformed to Groves' description. The fungus found widely distributed in the United States is undoubtedly *Septoria nodorum* Berk. Hence the nomenclature and synonyms are as follows:

Septoria nodorum Berk.

Septoria glumarum Pass.
Phoma hennebergii Kühn
Macrophoma (Cylindrophoma) hennebergii Berk. and Vog.

Fig. 2. Heads of "Red Wave" wheat heavily infected with *S. nodorum* Berk. Note numerous pycnidia on glumes.

Mycelium. The mycelium is colorless, 2-3μ thick, septate and very much branched. The walls are thin, and large vacuoles often appear in the older strands. In colonies on potato agar it is white, then light-olivaceous areas appear, and after a couple of weeks the surface of the media is almost black. In the host plants the mycelium grows rapidly and forms in clumps when forming the pycnidia.

Conidia. (Fig. 3, A.) Found only on oatmeal agar; oblong, cylindrical, entire, straight or slightly curved, rounded ends, hyaline, 3-septate, guttulate near septa, 2–4 x 18–32μ, averaging 3 x 24μ; produced laterally usually at the septa of germinating pycnospores.

Pycnidia. Pycnidia are seriately arranged or widely scattered, spherical, flattened or elongate, subepidermal, ranging in size from 160 to 210μ in diameter. The wall is thin, soft, and parenchymatous, at first light brown in color, later becoming dark brown or black. The ostiole is circular to oval opening between the guard cells of the stomata (Fig. 4).

Pycnospores. (Fig. 3 B, C.) Pycnospores are oblong, cylindrical, straight, curved or angularly bent, obtuse and rounded at the ends, hyaline, 3–septate, guttulate, 2–4 x 18–32μ, averaging 3 x 26μ. They emerge from the pycnidium in long serpentine strands. The spores are repelled from each other probably by surface tension phenomena.

Perithecia. This stage of the life history of the organism is imperfectly known. Voglino (36) cultured *Septoria nodorum* Berk. and succeeded in discovering perithecia in certain cultures that contained asci and ascospores which were hyaline and one septate. On the basis of this he identified the fungus as *Sphaerella exitialis* Morini. However, there seems to be some question if the ascospores may not have been somewhat immature. At least the evidence as brought out later indicates that the ascigerous stage may be a species of Leptosphaeria.

Davis (8) found some perithecia associated with pycnidia of *S. nodorum* which he described as having three-septate, hyaline spores and paraphyses, thus placing the organism in the genus Sphaerulina. The writer found some perithecia closely associated with pycnidia of *S. nodorum* Berk. on glumes of Red Wave Wheat in July, 1921 (Pl. XXXIIIA), and upon examination found the ascospores were three-septate and of a yellow olivaceous color which placed the fungus in the genus Leptosphaeria.

Through the kindness of Dr. J. J. Davis some of the material collected by him in 1916 was examined, also some of his permanent mounts of the fruiting bodies. In these mounts, structures similar to paraphyses were observed and examination of perithecia from the wheat leaves

collected by him also showed that paraphyses were present there (Fig. 5A and B). Accordingly, the organism should be placed in the family Pleosporaceae rather than in the family Mycosphaerellaceae, and in either the genus Metasphaeria or Leptosphaeria rather than in the genus Sphaerulina. The ascospores appeared hyaline and would consequently be placed in the genus Metasphaeria. However, comparisons were made with other species of Metasphaeria and Leptosphaeria in the herbarium and these ascospores were doubtfully hyaline. When it is considered that ascospores comparable to these in every way, except that they were colored, were found by the writer associated with pycnidia of *Septoria nodorum* Berk. it is quite probable that the fruiting bodies collected in 1916 by Dr. Davis were somewhat immature, hence not yet colored. Therefore, this form is probably a species of Leptosphaeria. The relation between this species and *Septoria nodorum* Berk. was not definitely proved because the ascospores were not viable, and on this account neither isolations nor inoculation experiments could be made.

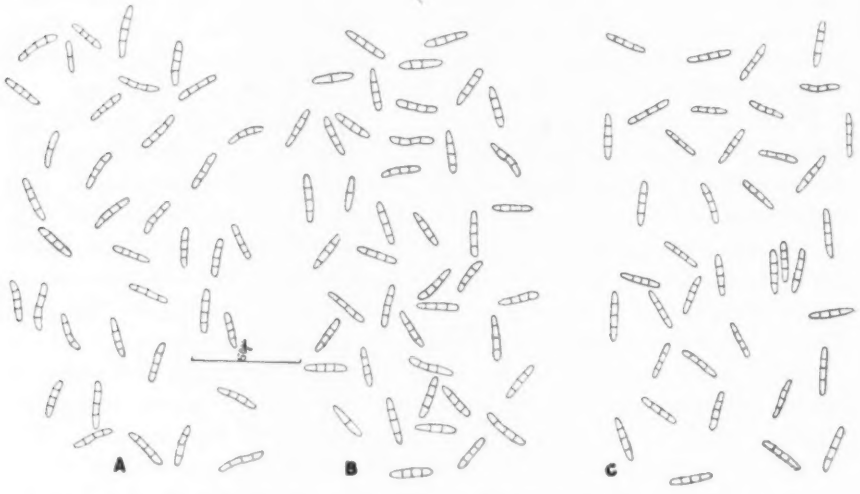

Fig. 3. Camera lucida drawings of spores of *Septoria nodorum* Berk. A. Conidia grown in culture. B. Pycnospores grown in culture. C. Pycnospores collected in the field.

The perithecia found by the writer in July, 1921, in the glumes of Red Wave wheat, were subepidermal, globose to subglobose, 40 to 140 mm. in diameter. The walls were thin, parenchymatous, black, and slightly raised. Ostiole circular to oval 18 to 24μ in diameter. Asci

cylindrical, hyaline, thin walled, rounded at end, eight-spored. Ascospores fusoid, ends rounded, 3-septate, slightly constricted at central septum, yellow to brown in color, 5 to 6 by 20 to 30μ. Paraphyses, cylindrical, rounded at tips, hyaline, septate, slightly longer than asci.

Physiology

Cultural studies. The organism was obtained in pure culture by isolating pycnospores. The pycnospores were obtained from the pycnidia in the glumes by soaking the infected glumes in water for a short period during which the pycnospores exuded through the ostioles in long threads. Single pycnospores were isolated on potato agar plates

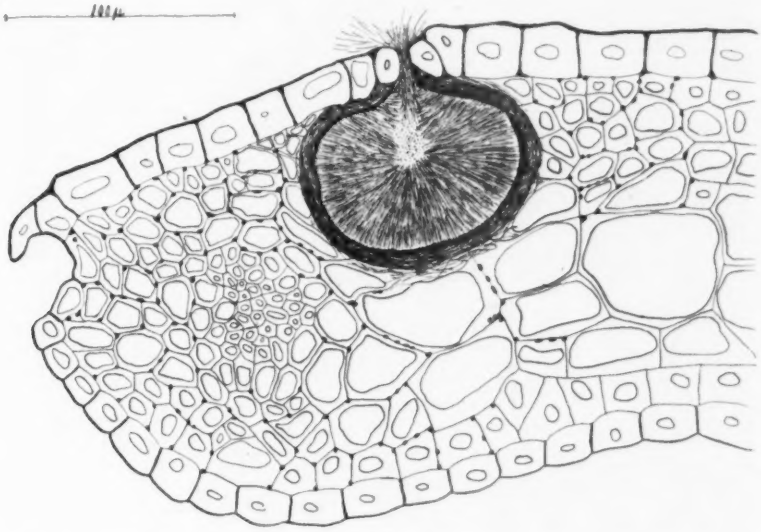

Fig. 4. Camera lucida drawing of a cross section of a pycnidium of *Septoria nodorum* Berk. Note ostiole under stomata. The black dots between the host cells are cross sections of fungus mycelium.

and upon germination were transferred to culture tubes for growth. The colonies developed into white masses of mycelium which grew quite rapidly making a thick, vigorous looking mat of mycelium. A number of different media were used as a source of nutrition for the fungus. Luxuriant growth was obtained on potato-dextrose agar, oatmeal-agar, wheat-extract agar, sterile oatmeal, cornmeal, bran, barley, wheat, sweet clover stems, alfalfa stems, wheat stems and wheat heads. Poorer growth was observed on Lima-bean agar and string-bean agar. The

potato-dextrose agar and oatmeal agar proved to be the best media, however, for the development of the mycelium and for the production of pycnidia. The pycnidia, which were produced only on these two media, appeared slightly imbedded in the media under the mycelium.

Pycnidia of *Septoria nodorum* were collected by the writer in July, 1921, at Madison, Wisconsin, on Red Wave wheat heads. In November, 1921, the pycnospores were obtained and germinated. Single germin-

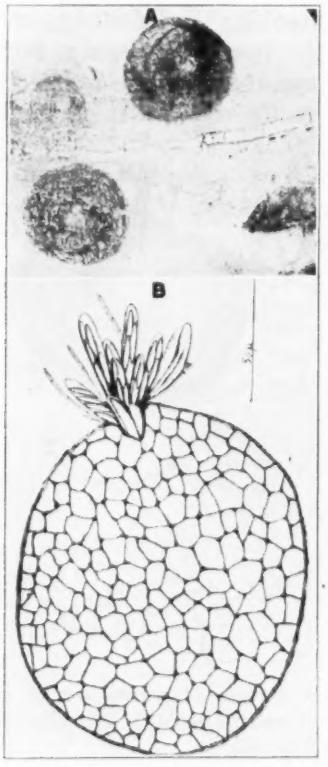

Fig. 5. A. Photomicrograph of perithecia found on a wheat leaf intermixed with pycnidia of *S. nodorum* Berk. B. Camera lucida drawing of a perithecium shown in A.

ating spores were tranferred to potato-dextrose agar slants for growth. In February, 1922, pycnidia containing pycnospores were discovered in many of the cultures. These pycnospores were germinated on potato-dextrose agar and oatmeal agar slants. A week later examination of the cultures showed that on the surface of 10 out of 14 of the oatmeal

agar cultnres conidia wete forming. They were scattered over the surface of the slant in small salmon-pink, circular, raised colonies (Pl. XXXIII, C). They compared favorably with pycnospores collected in

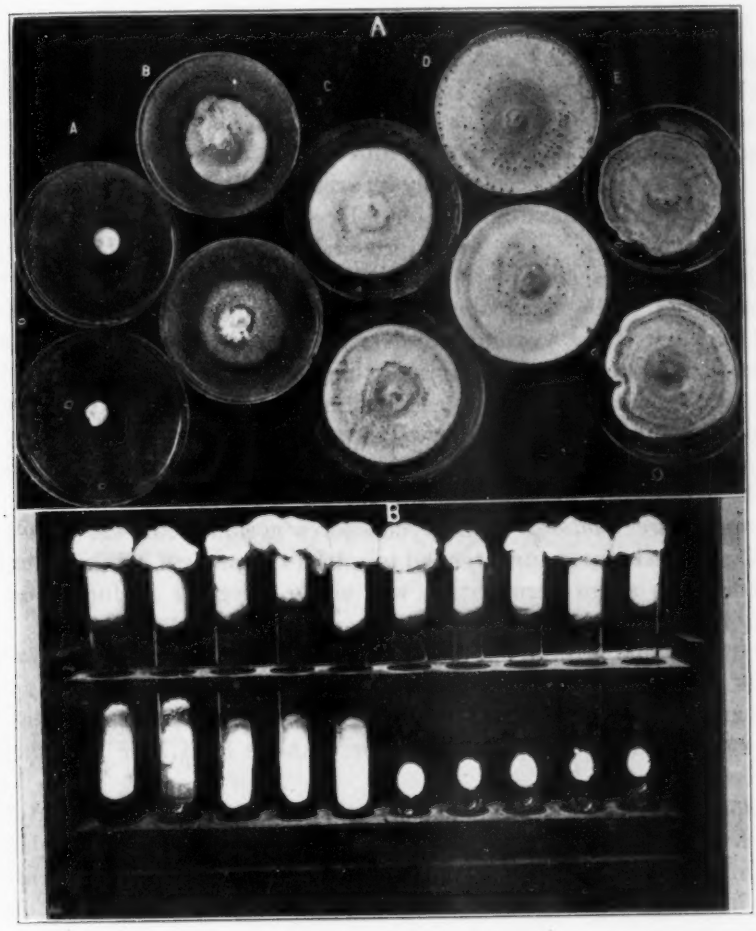

Fig. 6. A. Photomicrograph of *S. nodorum* after growing in plate cultures for 14 days at the following temperatures: A. 4–6° C.; B. 8–10° C; C. 14–16° C.; D. 20–24° C.; E. 28–32° C.

B. Growth of mycelium of *S. nodorum* Berk. on potato dextrose agar adjusted to pH 6.2 and pH 7.8 grown 10 days at room temperature.

the field as to size, septation, and shape. None of the transfers to other media developed conidia.

Conidia which were grown on oatmeal agar were transferred to a number of tubes of potato-dextrose agar and in every instance germinated by sending out germ tubes which branched profusely and formed a mycelial colony. After about one week numerous pycnidia began to form under the mycelium; the pycnospores were normal as to size, shape and septation.

Spore germination. The pycnospores of *Septoria nodorum* Berk. germinated best in water. In water and on agar poured-plates they formed germ tubes from one or more cells of the spore. The germ tubes branched and the colony developed into a white mass of mycelium. Voglino(36) stated that he occasionally secured conidia from the pycnospores when they were germinated in water. He shows figures of conidia formed from pycnospores. They were formed by the budding process very similar to that observed by the writer in a number of species of Septoria.

Ascospores. The ascospores of this organism have not been germinated by the writer. Voglino (36) described the germination of the ascospores of *Sphaerella exitialis* Morini, which he concluded were the perfect form of *Septoria nodorum* Berk. When he inoculated wheat plants with them pycnidia were developed. The ascospores germinate readily in water, they developed a short germination tube and then formed conidia on the sides of the germination tube.

Temperature relations. The pycnospores germinated best at about 20° C.; lower temperatures tended to retard the process, while at higher temperatures spore germination was either irregular in formation or prohibited altogether.

The mycelium growing on potato agar made the best growth between 20–24° C. The growth diminished toward the lower temperatures, very little growth taking place at 4° C. At 30° C. the growth was concentrically zoned and reddish-purple in color. Above 30° C. the growth was scant (Fig. 7 A).

Relation of reaction of media to mycelial growth. Bits of mycelium were transferred to potato agar slants which had been made to test pH 6.2 and pH 7.8. The fungus was grown for 12 days at room temperature. The difference is growth is shown in figure 6 B. Mycelial growth was greatly favored by a slightly acid medium.

Pathogenicity

Voglino (36) made a limited number of inoculation experiments on the different parts of the wheat plant with pycnospores of *S. nodorum* (*S. glumarum*) and found that the organism was pathogenic upon all parts of the wheat plant above ground, i. e., nodes, internodes, rachis,

glumes, awns, and leaves. Rosen (28) made some inoculations in the greenhouse and reported leaf and glume infections. In the investigations conducted by the writer all parts of the wheat plant have been infected by inoculation by pycnospores both in the greenhouse and in the field.

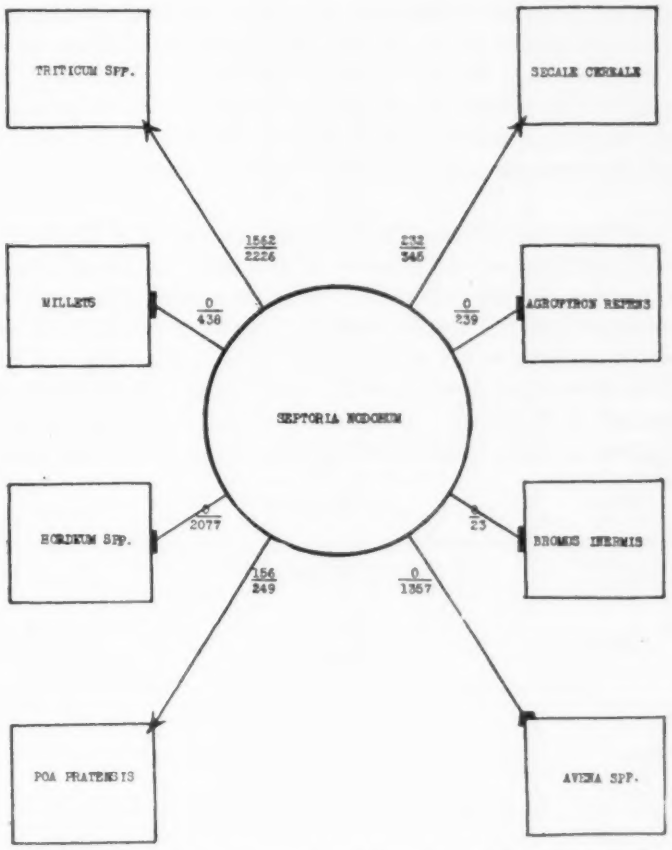

Fig. 7. Diagram showing source of inoculum (in the circle) and the hosts inoculated (in the rectangles). The denominator of the fraction designates the number of leaves inoculated and the numerator the number of leaves infected at the end of 14 days. Arrows alone indicate infections.

The pycnospores isolated from any part of the plant were identical in every way. Inoculation experiments were conducted by employing such isolated pycnospores. The disease was reproduced after two weeks showing up characteristically on the different parts of the plants. The

leaves, when inoculations were made in the field, became infected more readily than other parts of the plant. The reverse was found to be true with plants inoculated in the greenhouse. The glumes of plants inoculated in the greenhouse showed signs of the disease first, followed by a browning of the rachis and the upper internode. The organism was reisolated from the artificially produced diseased areas and it was similar in every respect to the one with which the inoculations were made.

Cross inoculations. In the review of the literature the host range of this organism was found to include practically all of the cereals. Experiments were conducted by the writer, in which 47 species of varieties of cereals and grasses were inoculated with pycnospores suspended in water.

The inoculum was obtained from wheat glumes and leaves collected in the field and from wheat glumes upon which the disease was artificially produced in the greenhouse. The pycnospores which exuded from the pycnidia of infected glumes soaked in water formed a spore suspension which was sprayed upon the plants with an atomizer. The inoculated parts were then covered with paper bags which were removed after from 48 to 72 hours. A summary of the data from these experiments is given in table 1 and is still further summarized diagramatically in figure 7.

TABLE 1

Summary of results from inoculating various grains and grasses with pycnospores of Septoria nodorum Berk.

Hosts	Source of inoculum[1]	Number of leaves	
		Inoculated	Diseased
Avena barbata	1	77	0
	2	17	0
	3	15	0
Avena brevis	1	98	0
	2	19	0
	3	19	0
Avena fatua	1	110	0
	2	42	0
	3	19	0
Avena nuda chinensis	1	79	0
	2	12	0
	3	17	0

[1] Sources of inoculum as designated in table 3 are as follows: 1. Wheat heads and leaves. 2. Rye leaves. 3. *Poa pratensis* panicles and leaves.

Hosts	Source of inoculum[1]	Number of leaves	
		Inoculated	Diseased
Avena sativa (Culbertson)	1	100	0
	2	54	0
	3	16	0
Avena sativa nigra	1	105	0
	2	14	0
	3	14	0
Avena sativa orientalis	1	79	0
	2	20	0
	3	20	0
Avena sterilis (a)	1	100	0
	2	11	0
	3	19	0
Avena sterilis (b)	1	100	0
	2	19	0
	3	18	0
Avena strigosa	1	103	0
	2	15	0
	3	16	0
Hordeum deficiens	1	94	0
	2	16	0
	3	22	0
Hordeum horsfordianum (Ore.)	1	102	0
	2	19	0
	3	22	0
Hordeum horsfordianum (S. Dak.)	1	99	0
	2	13	0
	3	22	0
Hordeum distichon erectum	1	100	0
	2	19	0
	3	21	0
Hordeum distichon	1	97	0
	2	8	0
	3	25	0

Hosts	Source of inoculum[1]	Number of leaves	
		Inoculated	Diseased
Hordeum distichon nutans	1	100	0
	2	58	0
	3	14	0
Hordeum vulgare coerulescens	1	69	0
	2	20	0
	3	22	0
Hordeum vulgare hexastrichum	1	104	0
	2	17	0
	3	15	0
Hordeum vulgare himalaya	1	151	0
	2	15	0
	3	26	0
Hordeum vulgare nigrum	1	106	0
	2	10	0
	3	19	0
Hordeum vulgare pallidum	1	113	0
	2	19	0
	3	18	0
Hordeum vulgare trifurcatum	1	193	0
	2	34	0
	3	38	0
Triticum aestivum (Marquis)	1	135	121
	2	62	58
	3	17	12
Triticum aest. lutescens (Harvest Queen)	1	100	23
	2	76	54
	3	18	14
Triticum aest. lutescens (Early May)	1	109	81
	2	55	20
	3	15	8
Triticum aest. miltura (Red Wave)	1	107	81
	2	59	39
	3	20	15

Hosts	Source of inoculum[1]	Number of leaves	
		Inoculated	Diseased
Triticum compactum	1	91	86
	2	48	26
	3	21	11
Triticum dicoccum barrum	1	88	71
	2	47	12
	3	24	12
Triticum dicoccum atratum	1	118	96
	2	21	14
	3	19	13
Triticum durum	1	90	74
	2	46	29
	3	21	11
Triticum monococcum	1	92	74
	2	52	21
	3	16	14
Triticum polonicum	1	95	82
	2	62	29
	3	15	8
Triticum spelta	1	132	119
	2	63	29
	3	21	18
Triticum turgidum	1	104	84
	2	33	23
	3	22	8
Secale cereale	1	225	150
	2	83	62
	3	37	20
Agropyron repens	1	137	0
	2	73	0
	3	24	0
Bromus inermis	1	23	0
	2	0	0
	3	0	0

Hosts	Source of inoculum[1]	Number of leaves	
		Inoculated	Diseased
Chaetochloa italica	1	37	0
	2	8	0
	3	16	0
Chaetochloa viridis	1	85	0
	2	16	0
	3	8	0
Echinochloa crus-galli	1	85	0
	2	16	0
	3	8	0
Panicum clandestinum	1	69	0
	2	10	0
	3	17	0
Pennisetum glaucum	1	56	0
	2	12	0
	3	18	0
Poa pratensis	1	192	72
	2	24	10
	3	21	14

It will be noted from the table that *Septoria modorum* will attack the wheat species, rye and blue grass, regardless of whether or not the inoculum was obtained from any one of the three hosts mentioned.

Seasonal Development

On leaves.—Infection takes place on the leaves at any time during the spring, summer or fall. In the early spring and late fall when the temperature usually falls to freezing during the night and the days are comparately warm, characteristic lesions on the leaves may be found; they are more or less circular, lighter colored and sparsely dotted with pycnidia. The pycnidia developed in the fall, contained pycnospores that germinated almost 100 per cent in the spring. The lesions formed in the spring slowly invaded the whole leaf and killed it. When the tillers began to shoot infections were observed on all leaves over two weeks old.

Heads.—Infection was not observed on the head until shortly after blossoming time which gave approximately a sixteen day incubation

period for the fungus providing inoculation took place from one to three days after the heads appeared out of the sheath. Infection on the heads was not confined to any definite month but rather took place at a certain stage of the development of the wheat plant. In the vicinity of Madison, Wisconsin, June and July were the two months during which most of the wheat heads become infected. The disease spreads rapidly from the time of first infection until the grain is cut.

Source of Inoculum

The sources of the inoculum are the pycnidia which are formed in the diseased areas on leaves, nodes, glumes and awns. The pycnospores exude readily when the pycnidia are held under moist conditions. Germination of the pycnospores takes place in a very few hours after they escape from the pycnidia.

Modes of Overwintering and Longevity of Spores

The pycnospores of the fungus live over the winter period, provided they are retained in the pycnidium. During the winter of 1920–21 some wheat heads, heavily infected with this disease, were placed out-of-doors in the early fall and spore germination tests were made twice a month from November, 1920, until May 1, 1921. The results showed that the spores retained germinating powers during the whole period with little or no variation. A series of tests were made from similar material collected at the same time and kept in the laboratory. The germination of the spores from the laboratory material decreased 40 to 50 per cent after four months and at the end of six months very little germination was obtained. More than 30 per cent of the spores from material placed out-of-doors showed germination after 18 months.

Modes of Dissemination

The fungus is no doubt distributed most extensively by the dissemination of the pycnidia in diseased tissue. Locally the spread is by means of pycnospores. The pycnidia are carried about on the straw and chaff by means of the wind and other agencies at threshing time and on the straw transported for feed and commercial uses. A large amount of diseased plant material is usually left in the field after cutting. This material disintegrates during the winter, liberating the pycnidia which are disseminated by such agencies as wind, rain, and flowing water. The pycnospores are killed very easily by drying and by direct sunlight so that when dry they play a very small part in the dissemination of the fungus.

Time of Natural Infection

The leaves become infected at almost any time after they unfold. Infection is most prevalent, however, during April, May, and October on the leaves, and June and July on the glumes.

Mode of Infection

The fungus enters the host plant by direct penetration of the cuticle. It then grows in between the epidermal cells into the parenchymatous tissue.

The pycnospores which become lodged on the epidermis usually lie lengthwise in the depressions directly above adjacent epidermal cells. They germinate and the germ tubes follow the depression for a short distance, then stop abruptly and penetrate the cuticle.

Period of Incubation

Under both field and greenhouse conditions it was found that the time from inoculation until the disease was produced, (bearing mature fruiting bodies) was from 12 to 16 days. Six or seven days after inoculation very faint blotches of slightly lighter colored tissue were observed scattered over the heretofore healthy leaf. These blotches became lighter and lighter after about the tenth day when they were quite yellow. At this time light brown dots, the young pycnidia appeared which enlarged and became black, in which condition they were mature. Occasionally more than 14 days were required for the production of mature pycnidia, but in these cases the temperature was below the optimum for the development of the fungus. The incubation period on the leaves and glumes was about the same while on the culms, nodes, and rachis it was a few days longer.

Pathological Anatomy

The hyphae which grow through the cuticle are very small. They enlarge somewhat after the cuticle is penetrated. They are about natural size when they grow between the epidermal cells. Branching of the hyphae was not observed until after they had passed through the epidermis and come in contact with the parenchymatous cells beneath. The hyphae usually branched and changed direction of growth at this point, extending in all directions on a plane parallel to the epidermal layer. Long strands were observed in the crevices formed by the epidermal cells running parallel with the vascular bundles in the leaf. Small branches developed perpendicularly and extended between the parenchymatous cells. Often a single host cell was formed, completely

encircled by several hyphae. Aggregations of hyphae in various stages of density were found in the substomatal spaces so that it was possible to follow the formation of the pycnidia in their development from a few strands of hyphae to the mature fruiting body. The pycnidia were found to develop only in the substomatal chamber with their ostioles directly under the stomata. The host cells adjacent to the pycnidia were usually obscured by the dense wefts of hyphae. Several layers of cells in close association with the pycnidia were dead and obscured in outline. The host cells in the vicinity of the invading hyphae appeared to be in a normal condition. They showed no effects of the parasite until almost all of the intercellular spaces contained numerous hyphae. The hyphae invaded the culm but no fruiting bodies were found in the internodes. They were found commonly on the nodes, however.

Effects on the Physiology of the Host.

Wheat plants which were severely infected with this organism were stunted in growth. Most of the tillers were killed when small, leaving only two or three to head. The heads were from ⅓ to ½ normal size and usually empty or contained only a few shrunken kernels. Light infection on the glumes did not materially affect the host as far as yield was concerned. Severe infection, however, when all the glumes were involved reduced the yield 50 per cent or more. The kernels that were formed were shrunken and light in weight. Leaf infection in severe cases reduced the healthy leaf area and as a consequence reduced the production of carbohydrates. Only when practically all the leaves were involved was the yield noticeably reduced. Infection on the nodes was thought by Sutton (32) to result in the most severe losses. He stated that the mycelium entered the vessels and plunged them up thus cutting off the upward flow of sap. As a result of node infection two conditions depending upon the time of infection arise. Severe leaf infection generally spreads to the nodes which results in the stunting of the plant and a loss in yield. When glume infection precedes node infection the plants are fully grown so that there is no loss of yield unless the glume infection is severe.

HOST VARIETAL RELATIONS

Voglino (52) conducted an inoculation experiment in which he sprayed pycnospores of *Septoria nodorum* (*S. glumarum*) on the heads of three kinds of wheat, namely, "Nostrale" a susceptible variety, and "Noe" and "Petaniello" resistant varieties. The "Nostrale," became heavily infected while the "Noe" and "Petaniello" remained free from the

disease. He explained that this resistance in the one case was due to the change of chlorophyll bearing tissue to mechanical tissue, and the germ tubes not finding a suitable substratum died.

In the investigations conducted by the writer all the species of *Triticum* were found susceptible to the disease, and species of *T. durum*, *T. aestivum*, *T. compactum*, *T. turgidum*, and *T. polonicum* were found more susceptible, however, than *T. spelta*, *T. monoccum* and *T. dicoccum*. The several varieties of *T. aestivum* showed no marked difference in susceptibility, no outstanding cases of resistance being noted. The different varieties of the other species were not grown.

SUMMARY

1. *Septoria nodorum* Berk. is widely distributed in wheat growing regions and is pathogenic on the heads, leaves and culms of wheat species and *Poa pratensis*, and leaves of *Secale cereale*.

2. The disease is of marked economic importance more or less locally. The symptoms are distinctive on the glumes and culms and somewhat obscure on the leaves unless pycnidia are present.

3. The fungus grows readily on various artificial culture media, but especially well on potato-dextrose agar. Mycelium, conidia, and pycnidia have been developed in culture.

4. The cardinal temperatures for growth are as follows: minimum 4° C.; optimum 20 to 24° C.; maximum 32° C.

5. The pycnospores if enclosed in the pycnidium remain viable over winter in the vicinity of Madison, Wisconsin.

6. The fungus enters the host by direct penetration of the cuticle.

7. Period of incubation is from 12 to 15 days. The hyphae are intercellular and the pycnidia are subepidermal under the stomata.

8. Severely infected plants are usually stunted, the culms are weak, and the heads are about one-half normal size.

9. All species of Triticum inoculated were found to be susceptible. *T. spelta*, *T. monococcum*, and *T. diococcum* were not as susceptible, however, as the other five species that were inoculated.

SPECKLED LEAF BLOTCH OF WHEAT

INTRODUCTION

A disease of wheat widely distributed and commonly known as "Leaf spot" or "Nebular leaf spot" caused by *Septoria tritici* Desm., is here called "Speckled leaf blotch" of wheat. This name is chosen on account of the characteristic, speckled appearance of the lesions caused by the

presence of the dark brown or black pycnidia in the light colored, dead leaf tissues of the lesions. This disease which is reported widespread in Europe, Asia, Australia, and America was found to be prevalent in the vicinity of Madison, Wisconsin. Observations made during the fall of 1920 in 50 different fields showed that every field of winter wheat visited was infected with this disease. The per cent of infected plants ranged from 10 to 100 per cent. It was found that a large number of seedlings were killed in fields where infection was severe. During the winter and spring many tillers were also killed; in these instances all of the leaf surface of the tiller was covered with pycnidia. The severity of this disease and the uncertainty of its relationship to similar Septoria diseases on cereals prompted these investigations.

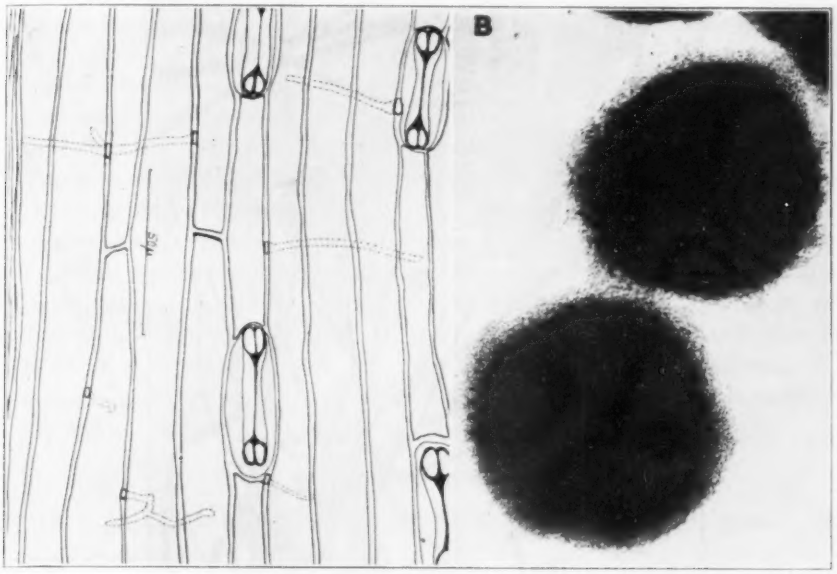

Fig. 8. A. Camera lucida drawing of surface of inoculated wheat leaf showing points of penetration by *S. tritici* and extent of growth at the end of about 60 hours. × 700.

B. Photomicrograph of two seven days old colonies of *S. tritici* on potato-dextrose agar.

THE DISEASE

Hosts

The host range of *Septoria tritici* Desm. is more or less limited, especially among the cereals. Desmazieres (10) first reported it on wheat

and Frank (14) reported it on "new grain" in November, as doing serious damage. Cavara (5) found the diseases on wheat doing extensive damage. Prillieux (27) and Tubeuf (34) both report the disease on wheat, Tubeuf having also found it on rye and certain wild grasses which he did not list by name. Pammel (23) and Cooke (6) report the disease in the United States on wheat and certain wild grasses. Sorauer

Fig. 9. A. Three month old winter wheat plant showing leaves (grouped to the right) killed by the fungus. B. Winter wheat plant showing the infected leaves tied in bundles November 1, 1920, also the small portions of the leaves that remained on April 1, 1921.

(31), Neuen-Lemarie (22), Ferrais (13) and Delacroix and Maublanc (9) report the disease at different times in different parts of Europe on wheat species only. Butler (4) reported the disease on wheat and some

wild grasses. Beach (1) reported the disease only on wheat species and certain grasses and stated that the disease would not go to rye, oats, or barley. The writer has conducted numerous experiments both in the field and in the greenhouse in an effort to determine further the host range. Up to the present time the hosts found susceptible to the disease are the wheat species, rye, and *Poa pratensis*. More than four thousand leaves of oats and barley of different species and varieties have been inoculated under various conditions of moisture and temperature, and at different times of the year, and in no case has the disease ever been reproduced on any of these species or varieties.

Geographical Distribution

This disease has been reported from most of the wheat growing regions of the world. Desmazieres (10) first described it from diseased wheat in France. Prillieux (27), Neuen-Lemarie (22), and Ferrais (13) all report the disease from parts of France. Passerini (24), Frank (14), Cavara (5), and Ferrais (13) report this disease from Italy. Frank (14) and Sorauer (31) report it from parts of Germany. Cooke (6), and Ferrais (13) report it from England, and Butler (4) reports it from parts of India and Australia.

The disease is well distributed over the United States. It was first reported by Pammel (23) and since that time by almost every experiment station in wheat growing districts. Beach (1) reports it very extensively around Urbana, Illinois. The writer has found this disease in every wheat field inspected in the vicinity of Madison, Wisconsin, and the causal fungus has been found to be in a viable condition on wheat plants at all times of the year.

Economic Importance

It is a difficult task to determine the loss caused by this disease. Only scattering reports can be found in the literature such as those given by Frank (14), Cavara (5), and Prillieux (27) who report serious losses from this disease in northern Italy. Butler (4) states that the disease does slight damages in India. In the United States no attempt has been made to distinguish between the diseases caused by *Septoria tritici* Desm. and *Septoria graminum* Desm. As a result, all reports of losses are published under the heading of Septoria leaf spot. The loss has been found to be greatest on seedlings in the fall and on tillers in early spring, 5 per cent of which have been found killed by this disease. The losses from the disease on other parts of the plant later in the season is negligible.

Symptoms

The symptoms are somewhat variable. In the fall when the disease first appears on the wheat seedlings it is conspicuous as more or less circular or oval irregular (nebula-like) spots scattered over the blades of the leaves. The center is usually somewhat light colored but still greenish and it shades off into the natural color of the leaf. The spot

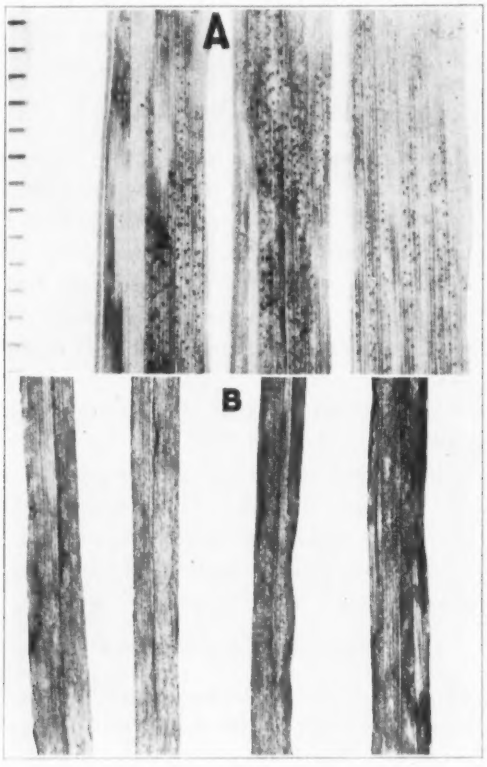

Fig. 10. B. Lesions (showing mottling and blotching as well as pycnidia) resulting from artificial inoculation in the greenhouse with pycnospores. A. Portions of heavily infected wheat leaves showing the mature pycnidia of *S. tritici*.

does not stand out prominently and were it not thickly dotted with prominent black pycnidia it would be almost unnoticeable (Pl. XXXIV). The disease remains in this form on the green leaves. It gradually spreads and finally involves the whole leaf blade by coalescing with other infection spots. Heavily infected leaves studded with pycnidia (Fig. 9 A) died prematurely. As the new leaves develop they become infected

also. In the spring after growth starts the spots gradually change to a more elongate or linear form, becoming reddish-brown in color. They finally become somewhat light colored in the olders areas (Fig. 10). The spot is at first more or less delimited by the larger veins. The entire leaf is finally involved. In certain severe cases of infection, there was not a square centimeter of healthy leaf blade tissue at blossoming time. The flag leaf and the next three leaves down the culm become completely involved in a very short time after once infected. They were prematurely killed, of a characteristic brown color, hanging down from the ligule; they became hard and dry and curled backward from each margin.

In the greenhouse the first symptoms that were detected on an inoculated plant appeared on the eighth day. At this time a slight, barely noticeable mottling of the previously uniform, green color took place. On the ninth day a decided yellowing was evident. After ten or eleven days the central portion of the light colored spot began to die and turn brown. At this time small, very light brown dots were detected in the lighter areas of the leaf, with the aid of a hand lens, After thirteen days the central portion of the spot was completely killed (Fig. 10 A), the pycnidia being plainly visible as brown dots. This is a description of one extreme, the other extreme is that the color of the infected areas remained green while the areas between the places of infection became yellow, light colored and finally died leaving the infected areas as "green islands" on the apparently dead leaf blade. These two extremes and all variations between were involved in the reproduction of the disease in the greenhouse.

CAUSAL ORGANISM

Taxonomy

Septoria tritici Desm. was described on wheat in 1842 by Desmazieres (10) in France. He gave a complete description of the organism and the disease. The next year he (11) described *S. graminum* on dry leaves of grasses (*in foliis siccis graminum*). This he described as very similar to *S. tritici*. In fact he regards these two species so similar as to include them later (12) under the same specific name, reducing *S. tritici* to varietal rank under the specific name *graminum*. This usage was subsequently followed by others and still others (5, 14, 20), have applied the species name alone (*S. graminum*) to the fungus on wheat. The distinguishing features between these fungi are, according to Desmazieres, that in *S. graminum* the pycnidia (called perithecia by him) are smaller (invisible) and closer together than in *S. tritici* and the

pycnospores are narrower and slightly enlarged at one end. He gave the length of the pycnospores of the two species as practically the same and did not give the exact width in either case. Passerini (24) gave the first complete measurements of *S. graminum*, stating that the pycnospores are from 1 to 1.25μ in diameter. Cavara (5) gave 1.5 to 2.0μ as the width of the pycnospores of *S. tritici*. Heretofore the size of the pycnospore has been the only means of distinguishing between the two organisms. Cavara (5) suggested that *S. graminum* and *S. tritici* were merely specialized strains of the same organism. Mangin (19) did not find *S. tritici* attacking wheat. He concluded that *S. graminum* was the only organism affecting wheat in France and that the pycnospores were often 2μ wide. Prillieux (27) and Ferrais (13), however, report *S. tritici* in France and give the diameter of the pycnospores as ranging from 3 to 5μ and 2.5 to 5μ respectively. Voglino (36) stated that these two species of Septoria would be separated only by artificial culture work. Beach (1) considered that the organism found in Illinois was morphologically more like *S. tritici* Desm. than *S. graminum* Desm. and that since *S. tritici* Desm. was the first described he called the organism he found in Illinois *Septoria tritici* Desm. Numerous collections have been made from wheat fields in this vicinity at all seasons of the year for the past two years and specimens have been sent from Virginia, Indiana, North Carolina, Kentucky, Alabama, Illinois, Kansas, Nebraska, Minnesota, North Dakota, South Dakota, Oregon, and California, and in all of this infected material were found lesions comparable to those of the type material of *S. tritici* and pycnospores that measured more than 1.5μ in diameter. The pycnospores measured on an average 2.5 to 3μ in diameter with extremes at 1.5μ and 4μ.

Through the kindness of Dr. Etienne Foëx of Paris, portions of the type material of both *S. tritici* and *S. graminum* have been examined. The type, *Septoria graminum* Desm., is distinct from species collected on wheat near Madison, Wisconsin. In the type material the lesions on the leaves are long, narrow and decidedly limited by the veins. The pycnidia are indistinguishable to the unaided eye except by careful examination.

They are seriately arranged parallel with the veins of the leaf. The pycnospores measured 1 to 1.5 by 30 to 50μ.

In contrast the Septoria lesions on wheat in this vicinity are circular to oblong, more or less limited by the veins. The pycnidia are readily seen without a lens and are more or less scattered. The pycnospores measure 1.75 to 3 by 40 to 75μ. By direct comparion it is evident that the Septoria organism on wheat in this vicinity is not *Septoria graminum* Desm.

On the other hand, type material of *S. tritici* Desm., furnished by Dr. Foëx compared very favorably with the organism found on wheat in this vicinity. The pycnospores from the type material measure 2 to 3 by 40 to 75μ and the pycnidia and lesions are very similar to those

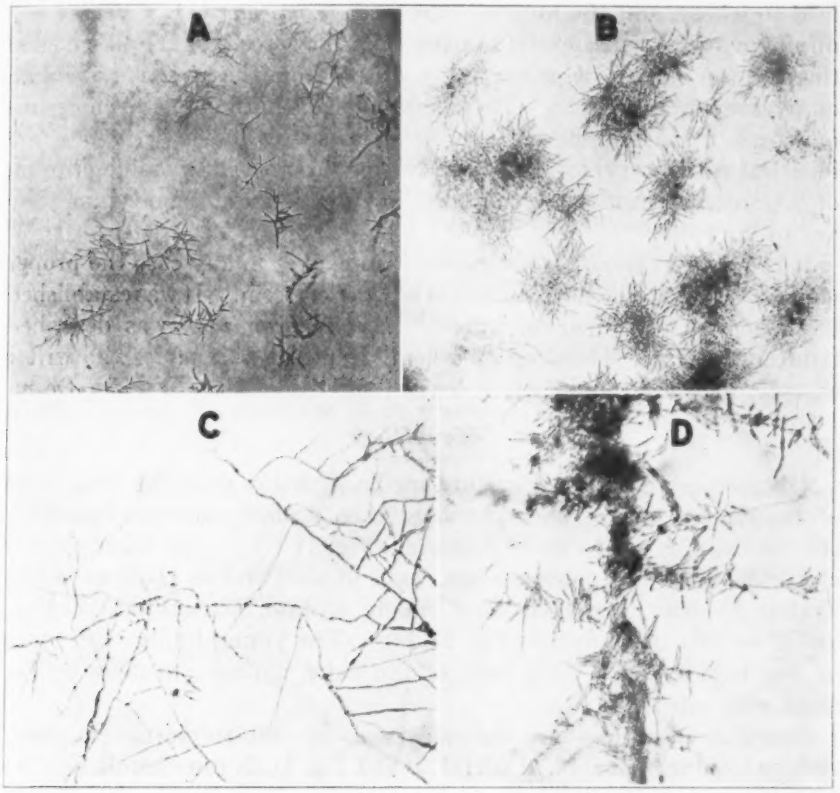

Fig. 11. Photomicrographs of *S. tritici* in artificial culture. A. Growth 24 hours after placing pycnospores on potato-dextrose agar. B. Same 48 hours later. D. Hyaline hyphae bearing conidia. C. Olivaceous hyphae from same colony partly shown in D.

found on the Wisconsin material. The two undoubtedly belong to the same species.

It is observed from the original description of Desmazieres (10) that *Septoria graminum* Desm. was not described on wheat; this is evident from the fact that the type material does not appear to be on wheat nor does the original description so state. Furthermore, Desmazieres (11) had previously described *Septoria tritici* on wheat. It seems probable

that he (12) established the species *S. graminum* to include Septorias with pycnospores very similar to the type found on many wild grasses. He then apparently chose the name *graminum* for the more generalized usage, since it seemed more appropriate for this than *tritici*. He then listed *S. triciti* as *S. graminum* var. *b. tritici* signifying a variety specialized to wheat, and the form on oats as *S. graminum* var. *c. avenae* signifying a variety specialized to oats. Desmazieres (10, 11) did not distinguish the varieties *b. tritici* and *c. avenae* from the type *S. graminum* on pycnospore characters. He gives only the length of the pycnospores of var. *b. tritici* and states that the pycnospores of var. *c. avenae* are identical with the type. However, it is noted in the original description of *S. graminum* that the pycnospores are a little more slender than they are in *S. tritici*.

It is apparent from the evidence at hand, that in any case the proper name to apply to the form on wheat is *S. tritici* Desm. It was established first and was described on wheat. *Septoria graminum* was described later and was not described on wheat. Hence in this paper the writer accepts, for the form on wheat leaves, the name *Septoria tritici* Desm.

Morphology

Mycelium.—In artificial culture media *S. tritici* develops two types of mycelium. One type is hyaline, thin walled, septate, branched, conidia bearing, 1.5 to 2μ in diameter (Fig. 11 C). The other type is olivaceous, black in dense masses, walls about twice as thick as in the hyaline hyphae, branched, more closely septate, non-conidia bearing, and 2 to 2.5μ in diameter (Fig. 11 D). The young hyphae are more or less homogeneous while cells of the older hyphae are more or less filled with vacuoles.

Pycnidia.—Pycnidia are subepidermal, in sub-stomatal chamber, globose to subglobose (Pl. XXXIII, B and Fig. 4), in rows parallel to the vascular strands (Pl. XXXV, A), brown to black, wall smooth, pseudoparenchymatous, 1 to 3 cells thick, 80 to 150μ in diameter. Ostiole circular to oval, slightly raised, 12 to 20μ in diameter.

Pycnospores.—Pycnospores are slender, cylindrical, straight or slightly curved, hyaline, 3 to 7-septate, ends rounded, contents homogeneous or slightly guttulate, 1.75 to 2.7 by 39 to 70μ, averaging 2.2 by 50μ for the summer spores, and 2.5 to 3.5 by 52 to 85μ averaging 3 by 76μ for the winter spores.

As noted pycnospores collected in winter have been found to be considerably larger than those collected in summer. Beach (1) was the first to record this. The writer has found that in winter the pycnospores average 1 to 1.5μ wider and 15 to 20μ longer than in summer.

In the greenhouse several pots of seedlings of *Triticum aestivum* (Marquis) were inoculated with pycnospores of *S. tritici* Desm. collected on winter wheat leaves in February. These pycnospores were distinctly longer and slightly thicker than pycnospores collected on wheat in July. Other plants were inoculated with the shorter pycnospores collected in July. Typical symptoms developed after eight or nine days and pycnidia were found on the blotches on the leaves after two weeks.

The symptoms developed on the two series of inoculated plants were similar. The lesions produced and the pycnidia formed were typical in both cases. Pycnidia and pycnospores were examined under the microscope and in both cases they were alike. The pycnospore measurements were within the limits given for summer spores and in no case were pycnospores found that compared in length with the pycnospores collected in February. These experiments confirm results obtained by Beach (1) who conducted similar experiments. It appears from these experiments, which were repeated four times, that the pycnospores of *S. tritici* Desm. are variable as to measurements at different seasons of the year. Table 2 shows the results of these experiments.

TABLE 2

Summary of inoculation experiments on Triticum aestivum showing type of pycnospore produced when "winter" and "summer" types of pycnospores were used as inoculum.

Date of inoculation	Number of leaves		Date of observation	Type of pycnospore	
	inoculated	diseased		used as inoculum	reproduced in new lesions
Feb. 10	24	18	Feb. 26	short	short
	25	20		long	short
	Controls	0		none	none
Feb. 20	20	20	Mar. 10	short	short
	14	12		long	short
	Controls	0		none	none
Feb. 27	18	16	Mar. 15	short	short
	23	20		long	short
	Controls	0		none	none
Mar. 4	10	10	Mar. 18	short	short
	15	14		long	short
	Controls	0		none	none

Conidia.—Conidia which resemble the pycnospores very closely have been noted on inoculated wheat leaves in the green house and in abundance on artificial culture media. From these two sources the conidia are almost indistinguishable. The conidia, first referred to by Janczew-

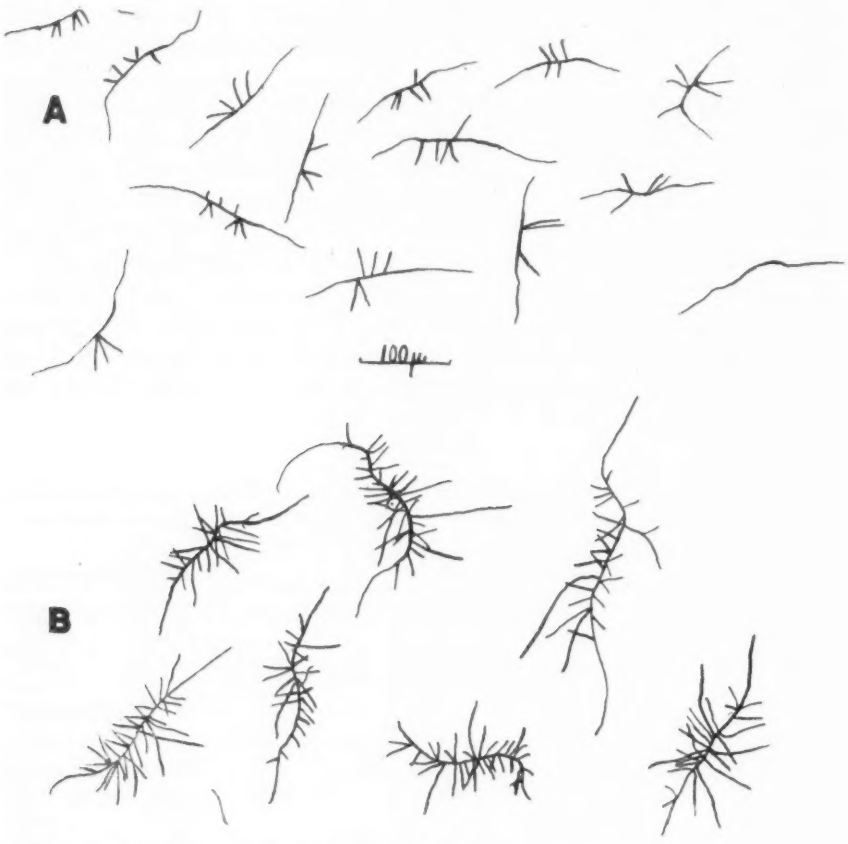

Fig. 12. Germinating pycnospores of *S. tritici.*
A. and B. Twenty-four and 48 hours growth respectively on potato-dextrose agar.

ski (17), are produced as secondary spores from the germinating pycnospores as shown in figure 14A and F. The conidia are cylindrical to fusiform, straight, or curved, ends rounded, hyaline, 3 to 7-septate, homogeneous or slightly guttulate to vacuolate, 2 to 3 by 35 to 65μ. They are pathogenic in a manner parallel to the pycnospores.

Perithecia.—Not known.

Physiology

Cultural studies.—Septoria tritici Desm. was secured in pure cultures on potato-dextrose agar by obtaining pycnospores from pycnidia collected on wheat leaves. The infected wheat leaves were soaked in water for a few minutes which caused the pycnospores to exude from the pycnidia. The spore suspension was then spread on the surface of slightly

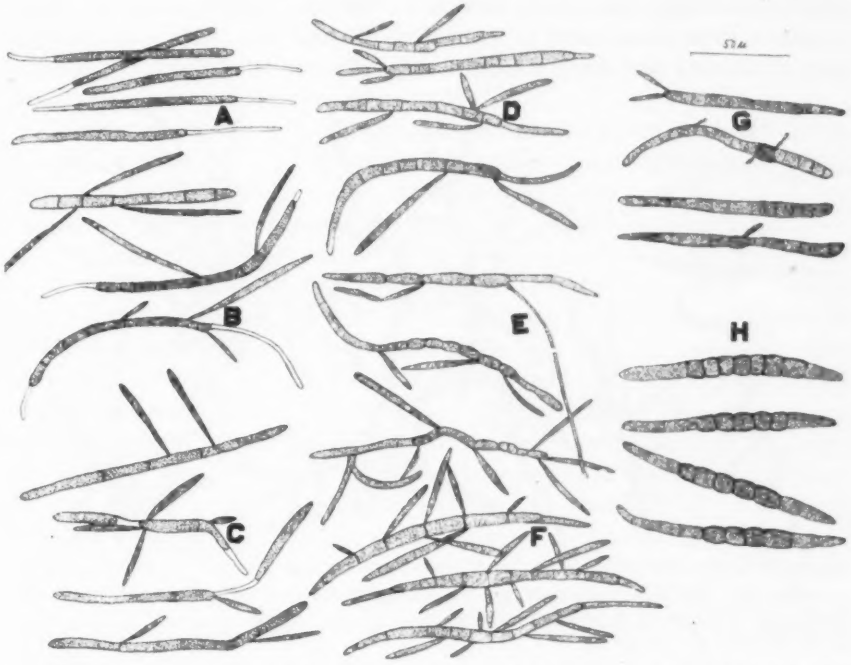

Fig. 13. Pycnospores of *Septoria tritici* suspended in water and incubated for 24 hours at different temperatures as follows; A. 2–3° C.; B. 7–8° C.; C. 10–12° C.; D. 14–16° C.; C. 18–20° C.; F. 22–24° C.; G. 28–30° C.; H. 32–36° C.

acidified potato-dextrose agar plates by means of a platinum loop. After incubation for 24 hours (Fig. 12 A), single, germinating spores were transferred to potato-dextrose agar in culture tubes. The colonies of conidia which developed for five days (Fig. 8 B) were pinkish or flesh colored, somewhat circular, convex, smooth, with a more or less irregular margin. This is in general agreement with conditions reported by Cromwell (7). After five to ten days mycelium was observed protruding from the margins of colonies. This mycelium was of two kinds (Fig. 11 C and D). One was straight, branched and hyaline, it produced lat-

eral conidia in great profusion but did not grow to any considerable length. The other developed at the same time or a few days later was somewhat coarser. The hyphae were undulating, branched, and of an olivaceous color. These hyphae grew rapidly and to considerable length, branched, and intertwined, forming a black mat of hyphae around the pink colonies. This dark colored mycelium did not produce conidia. After two weeks the surface of the colony began to turn dark colored and after four weeks it had a black stroma-like covering. Pycnospores were transferred to a number of different media and resulting growth showed strikingly different cultural characteristics. On potato-

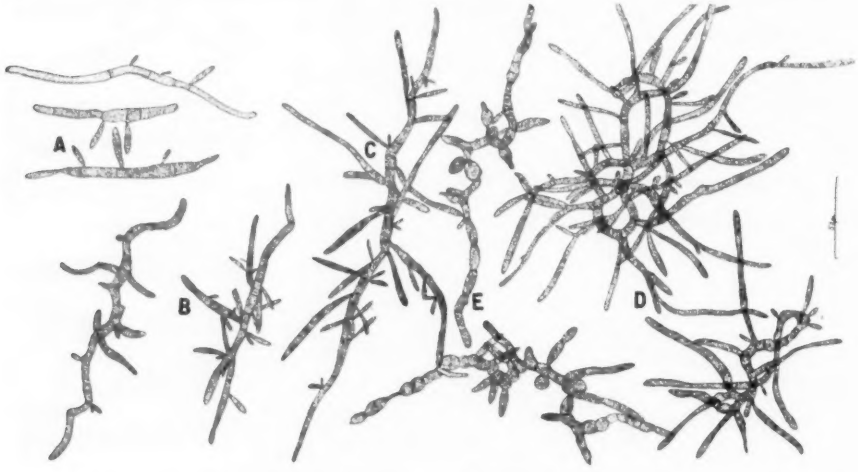

Fig. 14. Growth from pycnospores of *Septoria tritici* on potato-dextrose agar incubated 48 hours at different temperatures. A. 6–8° C.; B. 10–12° C.; C. 14–16° C.; D. 18–22° C.; E. 26–30° C.

dextrose agar the growth was very much as noted above except that after the first week the surface began to become wrinkled. The growth heaped up and formed folds (Fig. 15 A and B 3), later turning black. On nutrient agar no dark coloring took place, otherwise it developed very similar to the development on potato agar, but very much slower. On oatmeal agar the growth was similar to the growth on potato agar until the whole surface became black. White mycelium then began to to develop and after four weeks it had completely covered the black surface of the culture. Tranfers were made from the conidia and from the mycelium and after several successive transfers the cultures from conidia developed only conidia and those from mycelium developed only white mycelium. Pycnidia, containing pycnospores very similar

to those collected on wheat leaves, were developed on both potato and oatmeal agar cultures. Perithecia have not been found. Isolations from the large pycnospores developed in winter and those from the smaller pycnospores developed in summer are indistinguishable in culture.

Relation of temperature to growth in culture.—Pycnospores from wheat leaves were isolated and transferred singly to each of a number of potato agar culture tubes and incubated at different temperatures for ten days. The greatest amount of growth took place at from 20 to 24° C. Above and below this temperature the amount of growth was less; there was no growth below 6° C. nor above 32° C.

Relation of acidity and alkalinity to growth in culture.—Several series of test tubes containing 10 cc. each of potato-dextrose agar were made up, their hydrogen-ion readings ranging from pH 2.5 to pH 9.2. Conidia grown in culture were transferred to these agar tubes and incubated for twelve days. It was found that vigorous growth took place on all cultures in each series with pH readings between 3.8 and 8. Below pH 3.8 and above pH 8 growth was retarded. There was considerable difference in the color of the organism in the different cultures. The organism growing at pH 2.5 was of a vivid pink color and the one grown at pH 9.2 almost white. Different shades developed between these extreme colors, depending on the hydrogen-ion concentration. A band of black hyphae developed (Fig. 15 A) around the margin of the mass of pink spores in each of the cultures except at a pH of 9.2. This band became wider and more dense in the cultures of the series up to pH 6.2 where the maximum amount of black hyphae was produced. Toward the alkaline end of the series this black color diminished and at pH 9.2 there were no black areas whatever in the culture and spore mass was white.

Spore germination.—Conidia and pycnospores showed no difference in manner of germination. Conidia grown in culture behaved the same in germination as pycnospores grown in culture. In water there was evidence of germination after four hours. On potato-dextrose agar the spores enlarged considerably and from three to seven septa were evident after about six or seven hours. From 1 to 4 buds appeared close together along the sides of the spore, usually near the septa (Fig. 11 A). These buds developed into conidia-like bodies as described by Jaczewski (17) and after from 24 to 30 hours germinated. In this way colonies of conidia developed as previously described. Very scant mycelium was found at this time (Fig. 11 B). The mass of conidia became dense and heaped up as shown in Figure 8 B.

Relation of temperature to germination.—Series of germination experiments of pycnospores from wheat leaves were conducted in the different chambers of a graduated incubator both on potato-dextrose agar and in hanging drops of water. In each case the cultures were incubated for 24 hours, when certain observations and camera lucida drawings were made (Figs. 13 and 14). In the water cultures at the lowest temperature (2 to 3° C.) a hyaline tube, which appeared to be empty, had developed. Some swelling had taken place but no septa were visible. At 7 to 8° C. and at 10 to 12° C. a few conidia developed, but their formation was not regular, empty cells being frequently found. Some septation had taken place. At from 14 to 24° C. germination was more uniform. The conidia appeared to be normal and the septa were regular. At from 28 to 34° C. extensive swelling occured. There was also visible septation but little or no germination. Certain cells tended to become thick walled and chlamydospore-like, especially at the highest temperature (32 to 34° C.). The most favorable temperatures for germination in water were 22 to 24° C. Little or no germination took place at 2 to 3° C. or at 33 to 34° C. On the agar cultures the pycnospores germinated in much the same manner as they did in water, except that the germination seemed to be somewhat slower. The minimum, optimum, and maximum temperatures for germination were relatively the same in each case.

Pathogenicity

S. tritici is pathogenic on the leaves or leaf sheaths only of the host plants. Infected wheat plants have been collected during every month of the year. This disease was most destructive on seedlings of wheat upon which it has been found from the time they appear above the ground (Pl. XXXIV, A). The fungus will develop in late fall or early spring, when temperature conditions are not favorable for the rapid development of the seedlings. At this time the seedlings are rapidly overcome by the fungus and very often killed. The organism was isolated from wheat leaves in the usual manner. Several days after the pycnospores were transferred to culture tubes the colonies had spread over the surface of the agar and ten days after the cultures were made conidia were formed. The conidia were suspended in distilled water and sprayed by means of an atomizer on the leaves of wheat seedlings. The seedlings were kept in a moist chamber for three days immediately following inoculation and then removed to a greenhouse bench. Eight or nine days after inoculation a yellow mottling began to appear on the leaves and after 13 to 14 days mature pycnidia had developed on the yellowed

areas which began to die and become brown. Pycnospores, which compared in every respect with the pycnospores originally used, were isolated from the artificially produced pycnidia as formerly described. They were carried in culture with a parallel series of cultures from the original material and no differences were noted.

Cross inoculations with S. tritici.—Beach (1) conducted a number of inoculation experiments in which he used several cereals and grasses as hosts. He reported negative results however for all plants tried except *Triticum vulgare.* The writer conducted inoculation experiments both in the greenhouse and in field plots on about forty species of host plants including the cereals and certain related grasses. The inoculum in the form of a pycnospore suspension was applied by atomizers. The inoculated plants were covered with paper bags for periods of from 48–72 hours depending on weather conditions. The bags were then removed. The results are given in table 3 and shown diagramatically in figure 16.

TABLE 3

Summary of results from inoculating various grains and grasses with Septoria tritici Desm.

Hosts	Sources of inoculum[1]	No. of leaves		Hosts	Sources of inoculum[1]	No. of leaves	
		Inoculated	Diseased			Inoculated	Diseased
	1	153	0		1	179	0
Avena	2	21	0	H. v.	2	34	0
barbata	3	7	0	nigrum	3	8	0
	1	137	0		1	188	0
A. brevis	2	25	0	H. v.	2	36	0
	3	6	0	pallidum	3	15	0
	1	133	0	H v.	1	175	0
A. fatua	2	32	0	trifurcatum	2	28	0
	3	5	0		3	7	0
	1	152	0	Triticum	1	156	122
A. nuda	2	26	0	aestivum	2	33	17
chinensis	3	7	0	(Marquis)	3	15	9
	1	31	0	T. a. lutes-	1	158	121
A. sativa	2	14	0	cens (Har-	2	35	8
(C. I. 1375)	3	0	0	vest Queen)	3	13	4

[1] The sources of inoculum are as follows: 1. Pycnospores from wheat species. 2. Pycnospores from rye. 3. Pycnospores from *Poa pratensis.*

Hosts	Sources of inoculum	No. of leaves		Hosts	Sources of inoculum	No. of leaves	
		Inoculated	Diseased			Inoculated	Diseased
	1	28	0	T. a. miltura	1	136	103
A. sativa	2	131	0	(Red Wave)	2	23	13
(Culbertson)	3	9	0		3	9	7
A. sativa	1	126	0		1	149	82
nigra	2	39	0	T. compactum	2	36	17
	3	19	0		3	6	1
	1	137	0		1	142	95
A. sativa	2	19	0	T. dicoccum	2	24	11
orientalis	3	11	0	barrum	3	5	3
	1	118	0		1	197	139
A. sterilis (a)	2	28	0	T. dicoccum	2	32	12
	3	11	0	atratum	3	11	4
	1	12	0		1	140	102
A. sterilis	2	6	0	T. durum	2	26	13
(low belt)	3	7	0		3	15	9
A. sterilis	1	18	0		1	154	105
(Rust	2	11	0	T. monococcum	2	44	22
proof)	3	0	0		3	11	7
	1	173	0		1	160	108
A. sterilis (b)	2	22	0	T. polonicum	2	31	11
	3	10	0		3	12	5
	1	152	0		1	186	129
A. strigosa	2	22	0	T. spelta	2	31	10
	3	9	0		3	21	10
	1	149	0		1	148	115
Hordeum	2	29	0	T. turgidum	2	28	14
deficiens	3	10	0		3	7	4
H. horsfordianum	1	161	0		1	144	95
	2	30	0	Secale	2	49	40
(Oregon)	3	6	0	cereale	3	23	3
H. horsfordianum	1	167	0		1	166	0
	2	34	0	Agropyron	2	33	0
(S. Dak.)	3	8	0	repens	3	17	0

Hosts	Sources of inoculum	No. of leaves		Hosts	Sources of inoculum	No. of leaves	
		Inoculated	Diseased			Inoculated	Diseased
H. jubatum	1	79	0		1	14	0
	2	0	0	Agrostis	2	0	0
	3	12	0	platonifera	3	0	0
	1	173	0		1	10	0
H. distichon	2	31	0	Andropogon	2	0	0
erectum	3	11	0	nirtus	3	0	0
	1	165	0		1	14	0
H. distichon	2	26	0	Andropogon	2	0	0
nudum	3	9	0	sorghum	3	0	0
H. distichon	1	164	0		1	9	0
nutans	2	23	0	Arundo	2	0	0
	3	6	0	arenaria	3	0	0
H. vulgare	1	166	0		1	15	0
coerulescens	2	28	0	Astrebla	2	0	0
	3	10	0	triticoides	3	0	0
	1	152	0		1	7	0
H. v. hexa-	2	27	0	Avia	2	0	0
strichum	3	7	0	flexuosa	3	0	0
H. v. himalaya	1	147	0		1	91	0
	2	24	0	Bromus	2	11	0
	3	13	0	inermis	3	7	0
Chaetochloa	1	124	0		1	16	0
italica	2	17	0	Microlaena	2	0	0
	3	7	0	stipoides	3	0	0
	1	19	0		1	17	0
Chatocholoa	2	0	0	Panicum	2	0	0
viridis	3	0	0	brizanthum	3	0	0
	1	12	0		1	98	0
Cynosorus	2	0	0	Panicum	2	23	0
cristatus	3	0	0	clandestinum	3	6	0
Echinochloa	1	153	0		1	7	0
crus-galli	2	22	0	Panicum	2	0	0
	3	3	0	floridum	3	0	0

Hosts	Sources of inoculum	No. of leaves		Hosts	Sources of inoculum	No. of leaves	
		Inoculated	Diseased			Inoculated	Diseased
	1	14	0		1	125	0
Eschlaena	2	0	0	Pennisetum	2	17	0
luxurians	3	0	0	glaucum	3	9	0
	1	11	0		1	139	52
Festuca	2	0	0	Poa	2	31	12
arundinacea	3	0	0	pratensis	3	13	11
	1	14	0		1	8	0
Holcus	2	0	0	Poa	2	0	0
halepensis	3	0	0	trivialis	3	0	0
	1	9	0				
Lolium	2	0	0				
perenne	3	0	0				

Table 3 and figure 16 show that *Septoria tritici* is confined to the wheat species, rye, and *Poa pratensis*. This disease has been reproduced on these hosts consistently and has never been found on any of the other inoculated grains or grasses.

During October, 1920, several plants of each of 250 winter wheat varieties were inoculated with a pycnospore suspension of *Septoria tritici*. The inoculated wheat seedlings were covered with petri dish covers for 48 hours immediately after inoculation. Approximately two weeks after inoculation data were taken which showed 100 per cent infection in all varieties with the exception of five which had been destroyed by rodents.

CAUSAL ORGANISM IN RELATION TO THE PRODUCTION OF THE DISEASE

Seasonal development

During every month of the past two years viable pycnospores have been collected in the field in the vicinity of Madison, Wisconsin. There has always been an abundance of pycnidia on dead wheat leaves during the winter months. Early in spring when the winter wheat plants resume growth, the pycnospores which exude from the pycnidia as a result of the early rains germinate. Following infection irregular blotches appear on the wheat leaves. In these irregular, light colored blotches black, speck-like pycnidia form. As the wheat plants develop the

newly unrolled leaves become infected. In favorable springs, that is when there are abundant warm rains and foggy and cloudy days, the

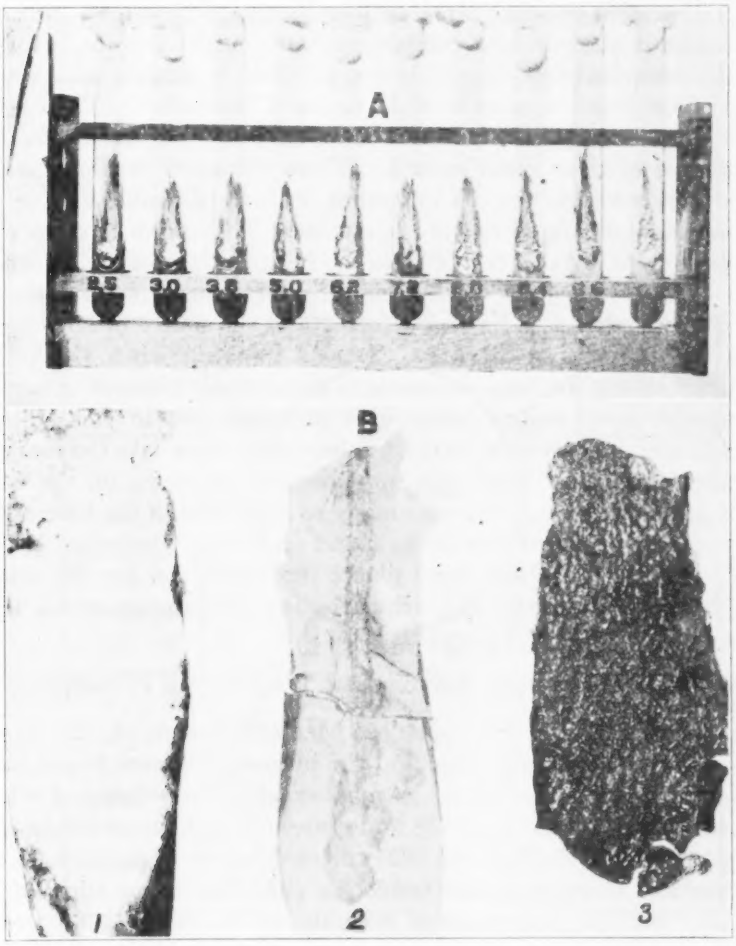

Fig. 15. A. Growth of *Septoria tritici* on potato-dextrose agar adjusted to different degrees of acidity and alkalinity from pH 2.5 to pH 9.2. Note blackening around organism at all except pH 9.2 (extreme right). B. Growth of *S. tritici* on different artificial culture media. Cultures incubated at room temperature for 28 days (removed from culture tubes). (1) On oatmeal agar; (2) On nutrient beef broth agar; (3) On potato-dextrose agar.

fungus invades the whole plant and sometimes kills it. When the culms lengthen infection usually decreases. However, in certain ex-

perimental plots of Blue Stem wheat during June, 1921, at Madison, Wisconsin, the spread of the disease on the plants was not lessened and at blossoming time every leaf including the flag leaf was entirely killed. This was possibly an exceptionally heavily diseased plot but nevertheless it showed how completely plants might become invaded. After the flowering stage very little new infection took place until volunteer seedlings began to appear in August and September. These seedlings became heavily infected but they were seldom killed by the disease because of their rapid growth. These volunteer seedlings which become infected from the old infections on old straw and stubble are very important in the spread of the disease. They serve to carry over the disease from harvest to the time the fall plantings of winter wheat are up. The seedlings of the fall plantings are usually sufficiently developed by October 1 to become infected and the source of infection is largely from volunteer seedlings. During late fall when the plants grow more slowly the fungus spreads to all parts of them and in certain experimental plots serious losses were observed due to this disease. Early fall plantings were injured to a less extent than late October and November plantings. Some loss was observed, however, on the early planted grain. In certain plots as many as 5 per cent of the tillers were killed but a whole plant was never found completely destroyed by the fungus. In late plantings small plants may be killed by the attack of the fungus; during the winter months the pycnospores retain their viability but the lesions do not enlarge.

Mode of Overwintering, Viability and Longevity of Pycnospores

As previously stated, the fungus has been collected during the winter months of two succeeding years and the pycnospores were found to be viable throughout the winter. A number of heavily infected wheat leaves were collected in July, 1920, and placed out of doors on the ground. During the winter of 1920 and 1921 infected leaves were taken to the laboratory and the pycnospores tested for viability. At no time during the winter did the percentage of germination fall below 86 per cent. The pycnospores, when retained in the pycnidia, survived the winter very readily.

The viability of the pycnospores was not materially changed during the fall, winter and spring months, but beginning with the summer months, when the pycnospores became a year old, some decrease in viability was observed. This decrease was not caused by the warm dry weather alone, because pycnospores collected in spring and kept during the summer showed no decline in viability. It was, therefore,

concluded that the age of the spore was an important factor in viability and that its decrease was due to age and warm dry weather together. Pycnospores kept in the laboratory in a pasteboard box showed a slight decrease in viability after six months. At the end of the year the per-

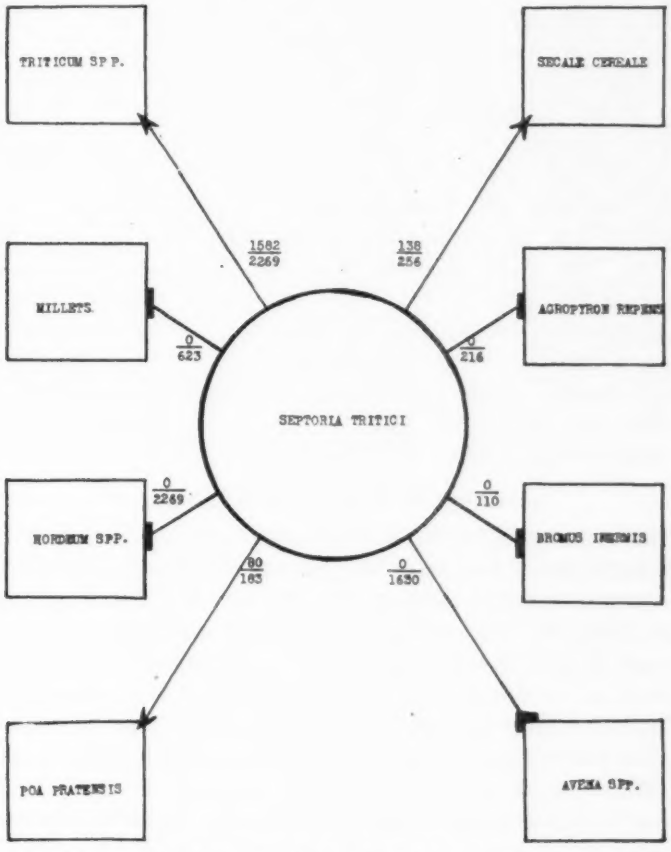

Fig. 16. Diagram showing results given in table 3. The source of inoculum is shown in the circle, the hosts inoculated in the rectangles. The denominator of the fraction designates the number of leaves inoculated and the numerator the number of leaves diseased at the end of 15 days. Arrows indicate infection.

centage of viable spores had decreased 50 per cent, and at the end of eighteen months to from 30 to 35 per cent. Sixty per cent of the pycnospores kept out of doors germinated after eighteen months.

Modes of Dissemination

On November 1, 1920, the dead plants of winter wheat heavily infected with *Septoria tritici* and thickly studded with pycnidia, were tied into small bundles with a cord. The leaves were left attached to the plant and the cord was tied to a firmly driven stake. On April 1, 1921, the bundles were collected. Instead of finding the leaves as they were left in the fall only short pieces were found which had been protected by the knot in the string and at which place the leaves had resisted disintegration by being closely packed together (Fig. 9 B). The parts of the leaves not held by the string had entirely disintegrated and were disseminated during the period between November 1, 1920, and April 1, 1921. The wind was probably the greatest agent of dissemination. It carries disintegrated leaf tissues containing pycnidia and the free pycnidia themselves. The wind, however, is probably not as important as rain in scattering the pycnospores. The wind may scatter the pycnidia over long distances and the rain by splashing the pycnospores enlarges the range of infection from a single pycnidium. The pycnospores become very evenly distributed during rainy days. The writer has observed that following such rains the prostrate leaves became more heavily infected than those that remain erect.

Time and Mode of Natural Infection

In the vicinity of Madison, Wisconsin, wheat plants have become infected during every month of the year except January and February. During the late fall and early spring the amount of new infection was less than during the late spring, summer and early fall.

The mode of infection was studied on leaves of wheat inoculated with pycnospores in the greenhouse. The leaves were sprayed with a water suspension of pycnospores of *S. tritici* by means of an atomizer. The plants were placed in a moist chamber immediately after inoculation and left there for 48 hours. They were then placed on a bench in a greenhouse kept at a temperature from 65 to 75° F. Every twelve hours for a period of six days after inoculation, pieces of inoculated leaves were placed in a solution of equal parts of 95 per cent alcohol and glacial acetic acid. They were left in this solution for at least 24 hours during which time the solution was changed once or twice. As a result the cells were killed with very little plasmolysis and the chlorophyll was removed. The pieces of leaf were white after 24 hours. They were then submerged for 15 or 20 minutes in Pianeze IIIb stain as used by Vaughan (35). The pieces were then washed in water and examined under the microscope. The pycnospores and mycelium were stained

a dark blue and the host tissue was slightly tinged red. By examination in this way the extent of growth and place of penetration were readily seen. After penetration had taken place the method of staining the leaf pieces was changed somewhat. The stain was diluted with three to five parts of 25 per cent alcohol, and the pieces of leaves were left in the stain for from 18 to 24 hours. This stained the whole pieces dark blue. They were then washed in water, passed through 95 and 100 per cent alcohol respectively and then put in carbol-turpentine to clear. When cleared the leaf pieces were passed through xylol and mounted in Canada balsam. The leaf tissue was slightly bluish-green while the fungus was a deep rose. The fungus was most easily detected on the surface of the leaf after it was washed in water and before it was placed in alcohol. When placed in alcohol the blue color of the fungus disappeared leaving it rose-red. Examination of a large number of pieces of leaf tissue prepared in this way showed that the germ tubes penetrated the cuticle at a point directly above adjacent walls of the epidermal cells. They grew down between the epidermal cells into the intercellular spaces. There was some evidence of stomatal infection but such instances were very rare and mycelium entering the stomata were not found directly connected to pycnospores of Septoria.

Period of Incubation

The incubation period varied from eleven to fifteen days depending upon environmental conditions. After inoculation no change in the host was observed from the normal until the sixth or seventh day. Yellowish blotches began to appear and after eight days the inoculated leaves became mottled. On the tenth day light brown specks more or less scattered over the light yellow blotch were observed by the aid of a hand lens. These specks, the pycnidia, darkened and finally became black. During May and June the period of incubation was the shortest observed, being only eleven days. The longest periods required for the reproduction of the disease was during the late fall when the temperature was comparatively low.

Pathological Anatomy

The study of the pathological anatomy of the disease was made possible by the use of Pianeze IIIb stain and methods already described. At the time the first symptoms appeared on the leaves it was found that the mycelium of the fungus had invaded a large portion of the light colored blotch. After penetration and growth down between the epidermal cells the hyphae branched and single strands often grew parallel

with the epidermis directly under it (Pl. XXXVI, A and B), in various directions but most commonly lengthwise of the leaf. The side branches followed very closely the wall of the cells that were adjacent to the epidermal cells. The septations and vacuoles in the hyphae were easily seen. Occasionally there was a weft of closely interwoven hyphae in the substomatal chamber. At this time these wefts were found to be made up either of one or two strands of hyphae which had branched once or twice, or of one or two closely interwined balls of hyphae situated directly under each end of the stomata in the substomatal chambers (Pl. XXXVI, B and C). The hyphal strands that grew deeper into the host tissue were rather irregular as to the direction of growth but they were always found in the intercellular spaces. It was observed that the hyphae grew through the tissue to the lower epidermis. Here they turned and grew parallel to the epidermis or turned back again and grew deeper into the tissue. No haustoria were observed. The spread of the fungus in the host tissue was more or less limited by the vascular bundles (Fig. 12 A). The hyphae appeared to be confined to the host tissue between the bundles except where the hyphae were very numerous, in which case certain of the bundles were killed. Under such conditions the hyphae were observed to grow across vascular bundles growing directly under the epidermis. When they were past the vascular bundle they branched profusely again and grew in all directions. Further examination of the diseased leaf tissues made at the time the pycnidia were mature showed that the pycnidia always occupied the substomatal chamber, so completely filling it as to occasionally crowd the parenchymatous cells that bordered on the substomatal chamber out of position. The pycnidia were more or less flattened on the top next to the epidermis. The ostiole which in culture was circular to oval conformed to the shape of the stomata and was without exception directly under it. The small oval to lentical shaped cells forming the pycnidial wall were compact. The outer cells were covered with mycelial strands connecting with the hyphae in the adjacent host cells. These host cells, a dozen or more in number, adjacent to the pycnidium, which were dead and in most cases collapsed and irregular in form, were penetrated by the hyphae. Adjacent to the dead areas host cells have been found in various transition stages from dead to healthy.

SUMMARY

1. Speckled leaf blotch of wheat caused by *Septoria tritici* Desm. is widely distributed in the wheat growing regions of the world. The disease also occurs on rye.

2. The disease is of economic importance, locally, during recent years especially on wheat.

3. The disease occurs only on the leaves of the host plants.

4. The ascigerous stage of the fungus is not definitely known.

5. The mycelium of the fungus is composed of branched, hyaline, septate hyphae. The pycnidia are subepidermal, subglobose, smooth, black. The pycnospores are cylindrical, septate, hyaline, 1.7 to 3.4 by 39 to 86μ. During the summer the pycnospores average 2.2 by 55μ and during winter 3 by 76μ.

6. The fungus grows well on slightly acid, potato-dextrose agar, producing mycelium, conidia and pycnidia.

7. Cardinal temperatures for spore germination are as follows: minimum 2 to 3° C., optimum 22 to 26° C., and maximum 32° C.

8. Cross inoculation experiments show *S. tritici* to be pathogenic on wheat species, rye and *Poa pratensis*.

9. The fungus overwinters in the pycnidial stage, the pycnospores remaining viable if retained in the pycnidia.

10. Infection takes place by direct penetration of the cuticle. The germ tube then grows between the epidermal cells and develops further between the cells of the parenchyma. Host cells are not penetrated until after they are killed.

11. The period of incubation is from 11 to 15 days.

12. The mycelium is intercellular, the pycnidia are subepidermal, in the substomatal chambers. The pycnospores escape through the ostiole.

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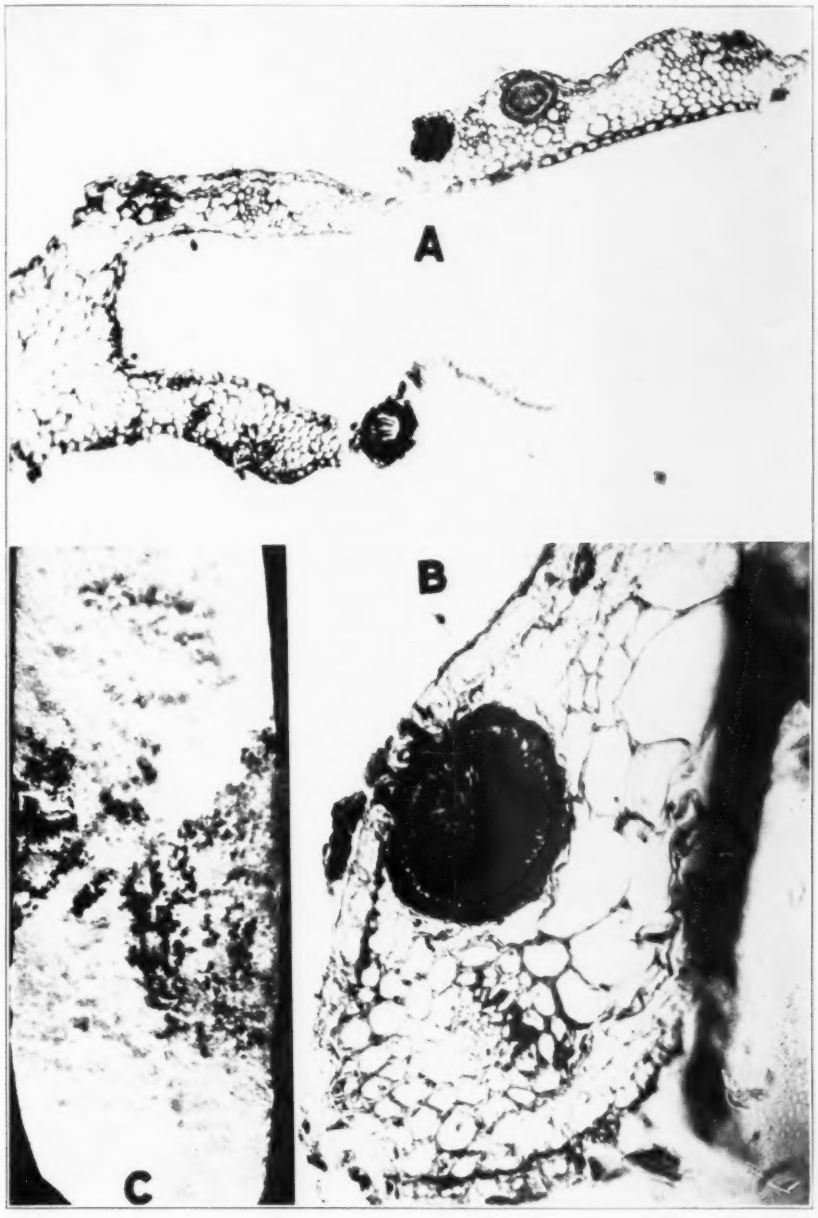

GLUME BLOTCH OF WHEAT

A. Photomicrograph of a pycnidium of *S. nodorum* Berk. in cross section and a perithecium (below).

B. Photomicrograph of cross section of a pycnidium of *S. nodorum* Berk. C. Culture of *S. nodosum* Berk. showing colonies of conidia intermixed with the white mycelium.

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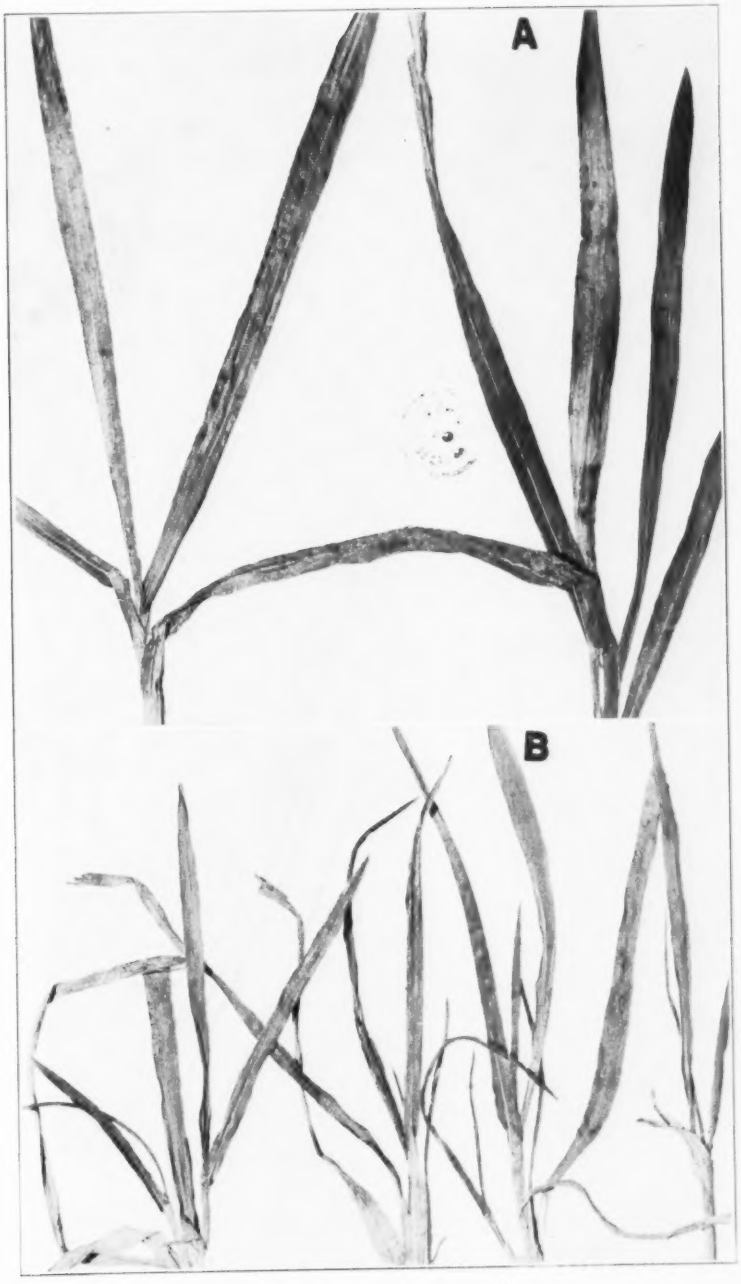

SPECKLED LEAF BLOTCH OF WHEAT

A. Tillers of winter wheat heavily infected. Seeds sown in August, 1920. Plants collected April 1, 1921. B. Seedlings of winter wheat heavily infected. Seeds sown in November, 1920. Plants collected April 1, 1921.

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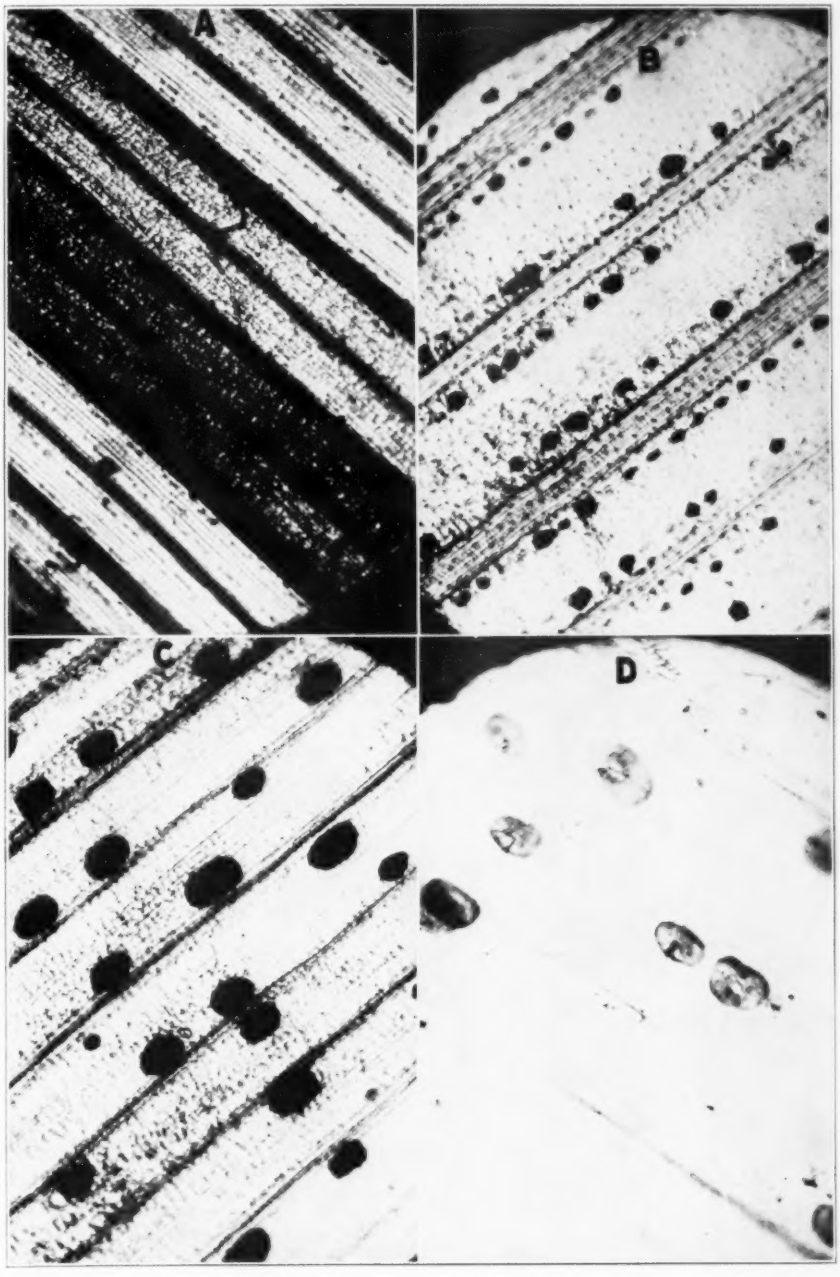

SPECKLED LEAF BLOTCH OF WHEAT

Photomicrographs of portions of wheat leaves infected with *S. tritici*. A. Showing tendency toward limitation of spread of infection by veins. 1, Uninvaded; 2, heavily invaded; 3, lightly invaded. B. Leaf sheath showing seriate arrangement of pycnidia. C. Leaf blade showing variations in shape and size of pycnidia. D. Showing pycnidia, ostiole and escaping pycnospores.

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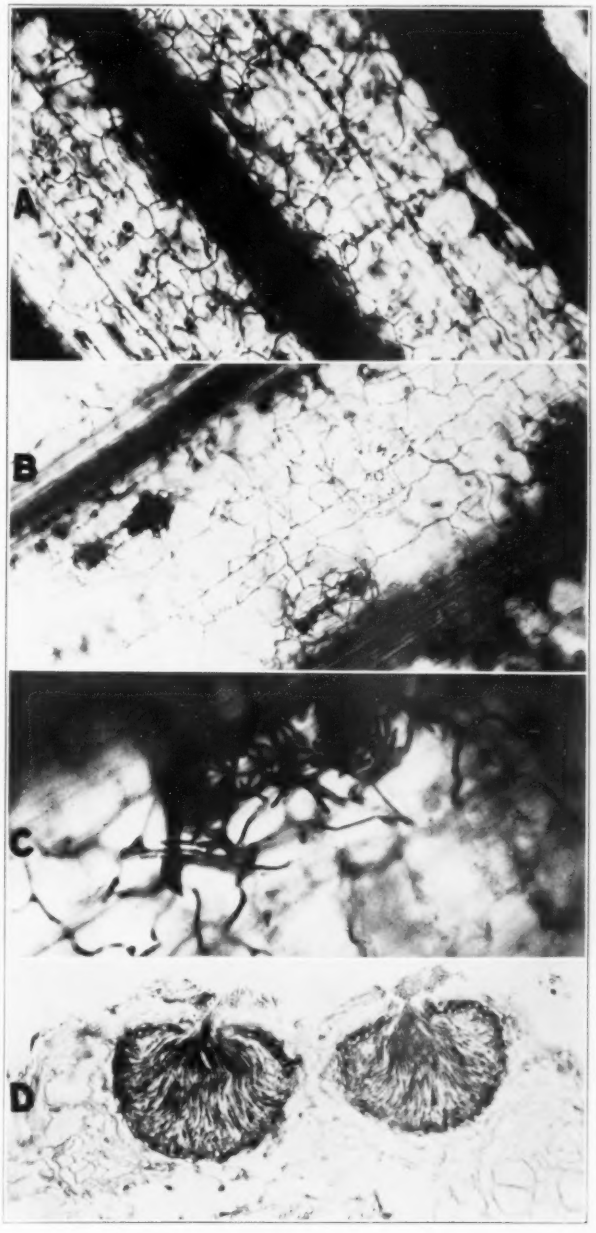

SPECKLED LEAF BLOTCH OF WHEAT

Photomicrographs showing hyphae and pycnidia of *S. tritici* in wheat leaves. A. Showing the hyphae among the parenchyma cells. B. Same as A, showing beginnings of formation of pycnidia below stomata. C. Aggregations of hyphae under a stoma —an early stage in the formation of a pycnidium. D. Cross section of two mature pycnidia imbedded in dead, shrunken host tissue.

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ERRATA

Page 165, line 1 of legend should read "Fig. 2. *Macrosporium carotae*. A. Stem of a mature carrot plant, etc."
Page 279, line 34, "not likely" should be "unlikely."
Page 281, line 13, "Bordeaux Burgundy mixture" should be "Bordeaux or Burgundy mixture."
Page 381, title heading "Roselinia" should be "Rosellinia."
Page 384, line 14, "Roselinia" should be "Rosellinia."
Page 385, page heading, "Roselinia" should be "Rosellinia."
Page 390, line 15 "sore" should be "spore."
Page 396, line 18, "citullina" should be "citrullina."
Page 397, line 11, "Masse" should be "Massee."
Page 434, line 22, "Edgertown" should be "Edgerton."
Page 499, footnote belongs to bottom of page 497.

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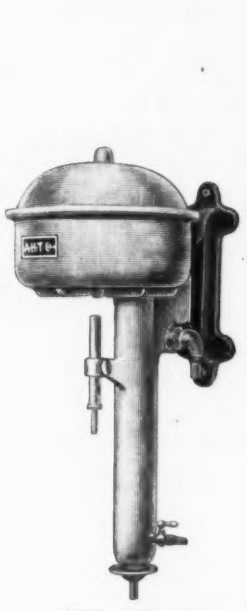

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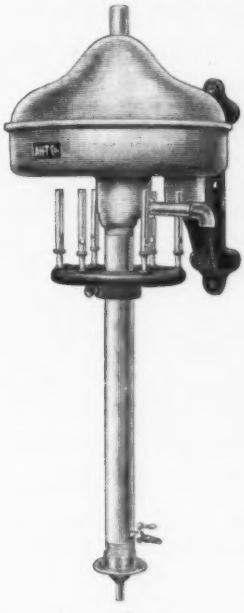

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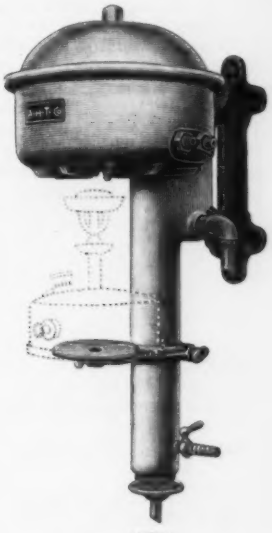

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